BEHAVIOURAL PLASTICITY OF LIFE HISTORY TRAITS IN THE NEW ZEALAND AVIFAUNA

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Abstract

The purpose of this research was to determine how predator control influences nest survival and changes in life history strategies of birds. All studies were conducted at two sites: one site had very little mammal control, while the other site is a "mainland island" in which all introduced mammals were trapped or poisoned. Nest survival rates of introduced and native species were compared between the two sites by locating and monitoring nests of 9 species. I found that mammalian predator control increased nest survival rates of both introduced and native species, but the increase of nest survival was more pronounced in native species. The influence of predator control on the plasticity of life history strategies in introduced and native New Zealand birds was also examined. Some life history strategies (e.g. time spent incubating, frequency of visits to the nest) changed significantly in the area with predator control, while other life history traits (e.g. clutch size) did not vary between areas. I found that both introduced and native New Zealand birds changed a variety of life history traits and that the changes were likely a plastic response to the recent change in predator numbers. As it has been suggested that birds may become less responsive to mammals when predators are controlled, I tested the response of birds to a model of a feral cat. Birds in the predator control area were significantly less likely to recognise the cat model as a potential threat. This suggests the recognition of predators can be rapidly lost from a population.

My research confirms that mammal control can increase nest success of native species, but reductions in predator numbers can also change a variety of life history traits and behaviours. As the removal of mammalian predators also appears to make birds less responsive to potential predators, it is important for continued mammalian control once management has begun. Otherwise, any reintroduction of predatory mammals into controlled sites would likely place such bird populations at greater risk as they would have behaviours suited to an environment with lowered nest predation risk.

Chapter 1

General Introduction

Predation plays an important part in the evolution of avian life history strategies (Lima 1987). Previously, it was thought that food limitation was the main factor shaping life history strategies (Martin 1987; Lack 1954). For example, clutch size in birds has long been considered to be limited to how much food is available during breeding and how many chicks a parent is able to feed (Lack 1954). However, other research has now confirmed that the risk of predation is also a major factor that can explain variation in life history strategies (Briskie & Sealy 1989; Conway & Martin 2000; Martin 1995; Skutch 1949; Yamaguchi & Higuchi 2005). Under this view, selection should favour behaviours and life history strategies that will lessen predation risk in order to increase overall survival and reproductive success.

Life history strategies are traits and behaviours that are typically thought to develop over evolutionary time, and thus the threat of predation should select for evolved defences and strategies to minimise the risk of predation (Lima & Dill 1990). However, there is evidence that birds are capable of monitoring their relative risk of predation at an individual level and then use this information for decision making which can cause changes in behaviour (Ghalambor & Martin 2002). For example predation risk can influence where birds decide to feed (Barta *et al.* 2004; Koivula *et al.* 2002; Suhonen 1993), where to nest (Forstmeier & Weiss 2004; Lima 1993; Morton 2005; Roos & Pärt 2004), and the extent of flocking behaviour (Beauchamp 2004). These short term changes in behaviour are termed behavioural plasticity. The ability to assess predation risk and change behaviour accordingly to reflect the current level of predation risk should be favoured by natural selection if such an ability increases survival chances. Recent research has shown that avian life history strategies are capable of changing in a matter of decades if there is enough selective pressure from predators (van Noordwijk 1980). However, it is not known if changes in life history strategies can occur at even shorter time intervals, or whether some species have more plastic responses as a consequence of their evolutionary history with predators.

The avifauna of New Zealand provides a unique environment for studying differences in life history strategies and how rapidly life history strategies might change. This is because New Zealand's birds evolved in an environment where the only mammals present were three species of bats (King 1984). The avifauna therefore filled the niches that would otherwise have been filled by mammals (Stevens *et al.* 1988). This also led to many species growing to large sizes, becoming mainly ground feeders, and inevitably losing the ability to fly (Diamond 1981). In contrast to continental areas where the main predators on birds were mammals and snakes, in New Zealand the only predators were other birds (Gill & Martinson 1991). Native birds were therefore unprepared for the arrival of humans and their mammalian cargo (Duncan & Blackburn 2004; Pierce 1986; Trevelyan & Read 1989). The arrival of humans and exotic predatory mammals caused the extinction of many bird species in New Zealand (Diamond 1986; Fleming 1962; Gill & Martinson 1991). New Zealand's birds did not evolve with mammalian predators and as a result did not have the same adaptations to avoid predators as their counterparts in continental areas (Lima & Dill 1990).

Humans brought many types of mammals to New Zealand that have become a threat to native birds. Mammals were brought for various reasons including hunting, food, and farming (King 1990; Parkes & Murphy 2003), but most have caused more harm than good. Introduced mammals negatively affect native birds by being both competitors and predators (King 1984). As a result, conservation measures in New Zealand are typically focused on recovering ecosystems by the removal of the introduced mammals (Atkinson 2001). Eradication of mammals on offshore islands has shown that recovery of bird populations is possible when mammals are removed (Clout 2001; Saunders & Norton 2001). However, on the mainland eradication is not possible but mammalian population control can still be undertaken to limit numbers. This strategy has been used to establish a series of "mainland islands", which are areas that have intensive mammal control measures including poisoning and trapping (Blair 2002). Intensive control of mammals during the breeding season of birds has shown encouraging results. For example, North Island kokako (*Callaeas cinerea wilsoni*) breeding success increases dramatically when predator control measures are taken (Innes *et al.* 1999) and kaka

(*Nestor meridionalis*) have also benefited from mammalian predator control (Moorhouse *et al.* 2003).

Mammals were not the only introduced animals to New Zealand; Europeans also brought many different bird species as well (Gill & Martinson 1991). In contrast to native New Zealand birds, European birds did evolve with mammalian predators and high predation rates. As a result the European birds have flourished while New Zealand birds have suffered from the introduction of exotic mammals (Moors 1983).

Outline of Thesis

The objective of my thesis is to compare the behavioural flexibility of life history traits in native and introduced bird species with regards to nest predation risk. It is expected that introduced European birds in New Zealand would be more plastic or flexible in their life history strategies than native New Zealand birds due to their differing evolutionary histories with high mammalian predation.

I start by firstly examining how predator control affect nest success of forest nesting passerine birds and whether this affects native species differently than introduced European birds. This was done by comparing the nest survival rates of 9 different species at two different study sites that differ only in the extent of mammalian predator control. Previous studies have shown that nest success of native endangered species are generally helped by mammal control during the breeding season, but few studies have examined how mammalian predator control affects birds that are more widely distributed in New Zealand and whether native birds are affected differently than introduced species. A study by Kelly *et al.* (2005) showed that stoat trapping can help bellbirds (*Anthornis melanura*) during the breeding season. This study showed a positive result for one common native New Zealand species; however it is not known how other common species respond to intensive predator management.

Next, in Chapter 3, I examine differences in life history traits between two study sites that differ in the level of predator control. Predator control in one study site has only occurred for the past three years; therefore unlike previous studies that have examined life history differences on an evolutionary time scale, any differences in life history traits and behaviour between my two study sites would have occurred in just the past three

years. Six main life history strategies were examined in this study and include changes in clutch size, the length of the incubation period, the length of the nestling period, the degree of incubation attentiveness, and rates of parental visitation during the incubation period and during the nestling period. I used both native and introduced birds to determine whether the life history traits of the introduced species were more "plastic" than the same traits in their native counterparts.

As birds that evolved on isolated islands like New Zealand generally do not recognise introduced predators, it is thought that the loss of such recognition is an evolutionary response to the decline in risk. In contrast, if an individual's ability to recognise and respond to a predator is also a plastic trait, which develops and is expressed only in environments where the chances of encountering predators are high, then removing predatory mammals from an area should cause birds to become less sensitive them. This hypothesis was examined in Chapter 4 by comparing differences in bird response between the two sites to a potential nest predation threat (a stuff feral cat placed near their nest). If birds become less sensitive to predatory mammals with their removal, this could have consequences on nest success and survival if mammalian control measures were then stopped.

Finally, in the last chapter I review the importance of mammalian control measures in New Zealand and how even common native New Zealand birds might benefit from mammal removal through increased nest success, but how at the same time, this may also place such populations under increased threat if such control measures are suddenly stopped. Implications of my results for the design of future predator control measures are also discussed.

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Chapter 2

Effect of predator control on nest success of native and introduced birds in New Zealand

Abstract

Introduced mammals are a serious threat to native New Zealand birds. Recently, a series of "mainland island" projects have been set up to control introduced mammalian populations. I compared survival of nests during the incubation and nestling stages in 5 species of native birds and 4 species of introduced birds in a mainland island near Kaikoura to determine if mammalian predator control affects native and introduced species differently. Comparison of nest survival rates between Waiman Bush (an area with extensive predator control) and Kowhai Bush (no predator control) demonstrated that mammalian predator control greatly decreased nest predation rate in both groups of birds. However, mammalian predator control increased nesting success significantly more in native species than in introduced species. My study confirms that mammalian predator control is an important device for helping the survival of native New Zealand birds.

Introduction

Many avian species of New Zealand are facing rapid population declines (Gill & Martinson 1991). One reason for these declines is the introduction of exotic animals (Gill & Hunt 1979; Holdaway 1999). Since humans arrived in New Zealand, at least 42 species of native birds have gone extinct and most of these extinctions can be attributed to the introduction of exotic mammals (Holdaway 1999). The native New Zealand avifauna evolved in the absence of mammalian predators, and as such does not have the proper defence mechanisms to deter or avoid these predators (King 1984). Introduced animals can also be competitors with the New Zealand avifauna. For example, since the introduction of exotic animals, populations of the kaka (*Nestor meridionalis*) have been decreasing; this species of native parrot must now compete with wasps (*Vespula germancia* and *V. vulgaris*) and possums (*Trichosurus vulpecula*) for food. However, a study by Wilson *et al.* (1998) discovered that although introduced animals can be competitors with the kaka, the main reason for their decline is due to predation by stoats (*Mustela erminea*). Overall, the introduction of predatory mammals has been disastrous to the avifauna of New Zealand (King 1984).

Mammals were not the only introduction to New Zealand; there was also a large influx of exotic European birds in the 19th century through the actions of the acclimatisation societies (Gill & Martinson 1991; Soper 1976). Unlike native birds, introduced European birds did evolve in the presence of mammalian predators in their native ranges (King 1984). As a result, they are likely to have many of the adaptations to avoid predators lacking in the native species, and it is expected that they would have higher nest survival rates as compared to native birds (Moors 1983). In other words, introduced birds should be able to cope with the pressures of high predation from mammals, and would possibly suffer less nest predation than native birds. However, there is little information available at present to test this idea.

Conservation in New Zealand has traditionally focused on controlling populations of introduced mammals, and in some cases, as in offshore islands, total eradication is possible (Atkinson 2001; Parkes & Murphy 2003). However, on the mainland, the populations of introduced mammals are so widespread that eradication is not possible. Nevertheless, in the last decade there have been attempts to control introduced mammals

on the mainland through continuous bouts of trapping and baiting with poisons (Clout 2001). These areas are often referred to as "mainland islands". This has become a popular and generally successful method for controlling introduced mammals (Saunders & Norton 2001). The primary predatory mammals controlled has varied from one mainland island to another but have included mustelids (*Mustela furo, M. erminea,* and *M. nivalis*), rats (*Rattus rattus*, *R. exulans* and *R. norvegicus*), possums, and feral cats (*Felis domesticus*).

Although a wide range of mammals have been introduced to New Zealand, the primary predators on birds are the mustelids, rats, possums and feral cats. Mustelids (stoats, ferrets, and weasels) are widespread across New Zealand and are probably the main predators on native New Zealand birds. Ferrets are larger than stoats and are capable of travelling up to 45km (Byron 2002). Weasels are not as abundant as stoats and ferrets; it is not known how significant a threat weasels are to bird populations but they are probably less important than stoats. Traps are used to control populations of all three species of mustelids (Blair 2002). Rats are also an important predator on many bird species. Their populations are mainly controlled by poisoning (Innes *et al.* 1995). Possums are a threat to native birds by being competitors as well as possible predators (Brown *et al.* 1993). Cats are another significant predator to New Zealand bird species. For example, cats were the cause of the disappearance of many bird species on Herekopare Island (Fitzgerald & Veitch 1985). The control of mammalian predators has usually been conducted at critical times in the lifecycle of each bird species, such as during the breeding season (Innes *et al.* 1999; Powlesland *et al.* 1999). For example, nesting success in the North Island kokako (*Callaeas cinerea wilsoni*) was significantly higher when there was active mammalian control present during breeding (Innes *et al.* 1999). Bellbird (*Anthornis melanura*) populations were also improved with the implication of mammalian predator control projects (Kelly *et al.* 2005).

Many researchers have found that predation rate is often highest on nests during the nestling period (Liebezeit & George 2002). This comes from the idea that the parents must visit the nest more frequently to feed the growing chicks (each visit potentially alerts a predator to the location of the nest), and the chicks become noisier as they grow, further drawing attention to the nest (Martin *et al.* 2000; Skutch 1949). However, other

studies have shown that there can be higher predation during the incubation period (Antonov 2004; Schaefer 2004). This could be due to the predators being able to locate conspicuous nests early in the breeding season, while the inconspicuous nests are capable of escaping predation, even if activity and noise around the nest increases (Ruxton & Humphries 2001). Furthermore, some studies have found no difference in predation rate between nests with eggs and nests with chicks (Farnsworth & Simons 1999; Schaefer *et al.* 2005).

The purpose of my study was to see if predator control in a mainland island in New Zealand increases nest survival rate. I measured nest success for each study species and compared differences in nest survival between two study plots; one plot had mammalian control in the form of poisoning and trapping while the other plot did not. The predation rates were then compared between native and introduced New Zealand birds. These comparisons were examined both within and between sites.

Methods

Study Sites

The study was conducted in the spring of 2004 and 2005 at two locations near Kaikoura, New Zealand: Kowhai Bush and Waiman Bush. Kowhai Bush (control site) is 240 ha of native woodland and has little mammalian predator control, except for some poisoning of possums around the eastern edges where the forest is adjacent to farmland. Waiman Bush is 100 ha of native woodland that has predator control for possums, cats, stoats, rats, and rabbits (*Oryctolagus cuniculus*). The predator control at Waiman Bush has only occurred for the past three years. The two sites are 5 km away from each other and experience similar climates, elevation and vegetation. Thus, the only significant difference between the two sites is the extent of mammalian predator control.

Description of mammalian predators

The mammalian predators that are present in both sites are possums, hedgehogs (*Erinaceus europaeus*), ferrets, stoats, cats, rats, and mice (*Mus musculus*). The brush-tail possum was introduced from Australia around 1858. They are opportunistic herbivores

who will eat small animals and eggs (King 1990). Rats are also present and are capable of eating eggs, nestlings, and killing adults. There are three species present in New Zealand (King 1990) but only ship rats and roof rats are present on the study plots (Moors 1983). Stoats are also a significant threat present in the sites. They were released in the 1880's to control rabbit populations, but also eat birds, mice, rats, possums, insects, and lizards. They are mostly nocturnal and locate prey by olfactory cues (King 1990); however they are also commonly seen during the day at Kowhai Bush. Feral cats are not as abundant in either of the sites, but can cause harm to the avian species when present. Ferrets are also present in the sites, but they are not as good climbers as stoats, so they may not be a significant threat to tree nesting bird species (King 1990). Hedgehogs are also common in both sites. Hedgehogs have not previously been thought as a threat to avian populations because they are thought to be mainly insectivorous. However, examination of stomach contents has shown remains of birds and eggs, revealing that hedgehogs will eat nest contents of ground-nesting birds when available (Jones *et al.* 2005). Hedgehogs could potentially pose a bigger threat to bird populations than was previously believed but are not likely to be important in my study as all the species I followed nest off the ground.

Predator control

Predator control at Waiman Bush was carried out from 2003 to 2005 primarily by Barry Dunnett and the local chapter of Forest and Bird, although I assisted with trap and bait maintenance. Fenn traps were set for mustelids, while leg hold traps or Gin traps were set to catch cats and hares (Blair 2002).

Poison was used in Waiman Bush to control the population of rats. The type of poison used was the anti-coagulant brodificum. The poison was placed in bait traps that were only accessible to rats, ensuring that only the rats were affected by the poison. The poison was first distributed just before the breeding season of the birds and restocking of the bait stations occurred at weekly intervals. It is important to have continual poisoning throughout the breeding season because rat populations can recover quickly after an initial poisoning (Innes *et al.* 1995). Both the traps and bait stations were positioned along trails throughout the study area. The distance between traps and bait stations

averaged about 50 m, which is similar to that used in other mainland island projects (Moorhouse *et al.* 2003; Saunders & Norton 2001).

Monitoring of nest success

Differences in nest success between the two sites were compared for each study species. The native bird species used for this comparison were fantails (*Rhipidura fuliginosa*), silvereyes (*Zosterops lateralis*), grey warblers (*Gerygone igata*), brown creepers (*Finschia novaeseelandiae*), and bellbirds. The introduced bird species used included blackbirds (*Turdus merula*), song thrushes (*T. philomelos*), redpolls (*Carduelis flammea*), and dunnocks (*Prunella modularis*).

Nests were located by watching adults and by searching vegetation. Nests were tagged nearby with flagging tape and then visited at intervals of 3 to 4 days until they fledged or failed. A nest was considered successful if young were observed leaving the nest or if the young were gone, but on the previous day they were ready to fledge (e.g. pin feathers unsheathed several centimetres). Nests were considered successful if at least one chick fledged. A nest was considered depredated if eggs or young were missing (before being capable of fledging) or if there were egg shells in the nest and the nest was destroyed. Mammalian predators were likely the main cause of predation. However, at some nests a series of peck marks could be seen on young dead in the nest. This was most likely due to the shinning cuckoo (*Chrysococcyx lucidus*), which has been observed destroying nests in order to force potential hosts to renest (J. Briskie, pers. comm.). As my study was concerned primarily with the effects of introduced mammalian predators, I did not include cases of cuckoo predation in the calculation of nest survival rates. When eggs or young were missing out of the nest, it was most likely from a mammalian predator. Although I could not determine if this was the case in most nests, avian predators (e.g. falcons, *Falco novaeseelandiae*) were rare on the study sites and are known to be a minor threat to most bird species in New Zealand (Franklin & Wilson 2003). Visitations to the nests by researchers have been suggested to increase predation, but little evidence has been found to date to support this possibility (Farsworth & Simons 1999; Keedwell & Sanders 2002; Mayer-Gross *et al.* 1997; Verboven *et al.* 2001).

However, visits to the nests occurred with the same frequency in both study sites to control for this potential bias.

Analysis

Survival rates of nests in the two study areas was determined by calculating daily survival rates and the combined probability of survival from the beginning of incubation until fledging (Mayfield 1961; Mayfield 1975). The analyses compared the predation rates between Kowhai Bush and Waiman Bush. A total of 925 nests were used for this analysis. This included a sample of 534 nests of introduced species and 391 nests of native species. In Waiman Bush, the number of nests followed for each species was: 50 fantail, 10 grey warbler, 16 bellbird, 9 brown creeper, 11 silvereye, 88 song thrush, 44 blackbird, 8 redpoll, and 11 dunnock nests. In Kowhai Bush, the number of nests followed for each species was: 75 fantail, 64 grey warbler, 48 bellbird, 26 brown creeper, 82 silvereye, 200 song thrush, 92 blackbird, 60 redpoll, and 31 dunnock nests. Differences in predation rates on introduced vs. native birds were also compared along with predation on eggs vs. nestlings.

Probability of survival during the incubation and nestling periods was calculated separately for each species using the Mayfield method (Mayfield 1961; Mayfield 1975). These probabilities were then multiplied together to get the overall probability of surviving the entire nesting period for each species. As my study was concerned with investigating if there are differences in mammalian predation on native and introduced birds, the probability of survival was calculated using only nest failures that resulted from mammalian predation. Thus, the results presented here are just the survival rates due to mammalian predation. Failures due to inclement weather or suspected avian predators (i.e., cuckoos) were similar in both study sites, and therefore do not bias the outcome of the calculations when excluded. Egg and nestling exposure days as well as the number of nest losses were summed in order to calculate overall survival rates in each study area. Introduced and native species were analysed separately. The probability of survival in introduced and native species was then combined in order to calculate the overall probability of survival in each site. The method suggested by Hensler and Nichols (1981) was used to test for significance between nest survival probabilities and to derive the

standard deviation. Not all species were included in some analyses due to small sample size.

Results

Nest Survival of Introduced birds

The overall probabilities of nest survival of introduced species in each study site are shown in Table 2.1. Blackbirds had significantly higher survival rates in Waiman Bush than Kowhai Bush ($z = 3.25$, $p = 0.0012$). Song thrush nest survival was also significantly higher in Waiman Bush than in Kowhai Bush ($z = 10.40$, $p < 0.0001$). However, redpolls ($z = 2.69$, $p = 0.0071$) and dunnocks ($z = 2.49$, $p = 0.013$) had significantly lower survival rates in Waiman Bush than Kowhai Bush. This is likely due to the small sample size of these species in Waiman Bush. Furthermore, many redpoll nests in this area were inaccessible making it difficult to determine either their nest contents or their outcome. Thus, in many nests it was not possible to determine the number of egg or nestling exposure days, and the resulting small sample size probably reduced my ability to accurately calculate the survival probability of Waiman Bush redpolls and Waiman Bush dunnocks.

To determine whether nest survival differed between the incubation and nestling period of each species in each of the two study areas, I divided my nest survival estimates into the two stages of the nesting cycle (Table 2.2). In Waiman Bush, blackbirds ($z = 0.92$, $p = 0.36$) and redpolls ($z = 0.85$, $p = 0.39$) did not differ significantly between the two stages. However, dunnocks ($z = 4.11$, $p < 0.0001$) and song thrushes ($z = 4.94$, $p < 0.0001$) had significantly higher rates of survival during the incubation period. In Kowhai Bush song thrushes ($z = 0.37$, $p = 0.71$) showed no difference in survival between the incubation and nestling period. While blackbirds ($z = 2.55$, $p = 0.011$) and dunnocks ($z = 3.41$, $p = 0.0006$) both had increased survival during the incubation period, redpolls had increased survival during the nestling period ($z = 4.38$, $p < 0.0001$). Kowhai Bush and Waiman Bush dunnocks had no difference ($z = 0.21$, $p = 0.83$) in incubation survival, however Kowhai Bush dunnocks had slightly higher survival during the nestling stage than Waiman Bush dunnocks ($z = 1.91$, $p = 0.056$).

Nest Survival of Native birds

The overall probabilities of nest survival of native species in each study site are shown in Table 2.1. Brown creepers had a significantly higher probability of nest survival in Waiman Bush as compared to Kowhai Bush ($z = 5.19$, $p < 0.0001$). Bellbirds ($z = 20.16$, $p < 0.0001$), fantails ($z = 1.95$, $p = 0.051$), and silvereyes ($z = 8.31$, $p < 0.0001$) also had significantly higher nest survival in Waiman Bush than Kowhai Bush. Almost all study species of native birds in Waiman Bush had significantly higher nest survival rates compared to their Kowhai Bush counterparts except for grey warblers ($z = 0.98$, $p = 0.33$) which showed no difference in nest survival between the study sites.

Nest survival estimates were divided into the two stages of the nesting cycle in order to observe any differences in survival between the incubation and nestling stage for each native species (Table 2.2). In Waiman Bush only fantails showed a difference in survival rates between the two stages. Fantails in Waiman Bush had significantly higher survival during the incubation stage than the nestling stage ($z = 6.29$, $p < 0.0001$). Brown creepers ($z = 0$, $p = 1.0$), bellbirds ($z = 0.65$, $p = 0.51$), grey warblers ($z = 0.41$, $p = 0.68$), and silvereyes ($z = 0.93$, $p = 0.35$) in Waiman Bush did not differ significantly between the incubation and nestling period. Kowhai Bush fantails showed the same trend as their Waiman Bush counterparts with significantly increased survival during incubation as compared to the nestling stage ($z = 2.0$, $p = 0.046$). Grey warblers ($z = 2.89$, $p = 0.0039$) and bellbirds ($z = 4.5$, $p < 0.001$) in Kowhai Bush also had significantly higher survival during the incubation period. However, brown creepers ($z = 7.87$, $p < 0.0001$) and silvereyes ($z = 4.46$, $p < 0.0001$) in Kowhai Bush had significantly increased survival during the nestling period.

Nest survival in Kowhai Bush and Waiman Bush

Introduced species in Kowhai Bush had significantly higher ($z = 3.81$, $p = 0.0001$) nest survival rates than Kowhai Bush native species (Figure 2.1). The survival estimates of all the introduced and native species in Kowhai Bush were compared to see if there were any differences in survival between the two nesting stages for each group. However, neither introduced ($z = 0.71$, $p = 0.48$) nor native species ($z = 0.36$, $p = 0.72$) in Kowhai Bush showed any significant difference between the incubation and nestling stages

(Figure 2.2). The introduced and native species survival estimates were combined to determine if there is an overall difference in survival between the incubation and nestling period in Kowhai Bush (Figure 2.3). However, there was no significant difference in the incubation and nestling periods when all species were combined in Kowhai Bush ($z = 0.24$, $p = 0.81$).

Native species in Waiman Bush had significantly higher ($z = 8.1$, $p < 0.0001$) nest survival than Waiman Bush introduced species (Figure 2.1). Nest survival estimates were divided into the nesting stages for the introduced and native species in Waiman Bush to determine if there are survival differences between these two periods. Introduced species in Waiman Bush had significantly higher ($z = 5.25$, $p < 0.0001$) survival during the incubation period (Figure 2.2). Native species in Waiman Bush also had significantly higher ($z = 3.51$, $p = 0.0004$) survival during the incubation period than the nestling period (Figure 2.2). The introduced and native species survival estimates for the incubation and nestling period were combined in order to determine if there are overall differences in survival between the nesting stages in Waiman Bush (Figure 2.3). There was significantly higher survival during the incubation period than the nestling period when introduced and native species survival estimates from Waiman Bush were combined ($z = 8.66$, $p < 0.0001$).

Figure 2.4 shows the change in nest survival between the two study sites for individual species. Overall, the native species showed a greater amount of change in nest survival from Kowhai Bush to Waiman Bush. The introduced and native species survival estimates were pooled together in order to determine if there is an overall pattern observed in nest survival between the two study sites. Figure 2.5 shows that there was significantly higher nest survival in Waiman Bush as compared to Kowhai Bush ($z = 29.19$, $p < 0.0001$).

Discussion

My results show that there is a difference in nest survival rates between Kowhai and Waiman Bush when mammalian failures were used to calculate the probability of survival. Although I did not directly estimate predator abundance, these results suggest there was a difference in mammalian predator abundance between these two sites as

would be expected from the intense level of trapping and poisoning that was carried out in the Waiman Bush site. My results also showed that there was significantly higher nest survival among native birds in the Waiman Bush population as compared to the introduced birds. This result suggests that native birds are more vulnerable to introduced mammals, and that when mammals are controlled, it is the native birds that benefit more (in terms of higher nest success) than the introduced species.

Probability of Nest Survival in Introduced birds

Waiman Bush song thrushes and blackbirds had higher probabilities of nest survival than their Kowhai Bush counterparts. These results show that the mammalian predator control in Waiman Bush has helped increase these two species chances of their nests surviving the breeding period.

However, there were two introduced species that had higher nest survival rates in Kowhai Bush than Waiman Bush. This was seen in redpolls and dunnocks. Many of the redpolls found in Waiman Bush were very difficult if not impossible to look inside to see the contents. This then lead to there being very low egg and nestling exposure days and many unknown outcomes. There was also a low sample size of redpolls found in the two years of this study. This would bias the result because any failure by a mammal that was documented would have had more of an impact on the result since exposure days were low. It would be beneficial to obtain larger sample sizes for Waiman redpoll populations and to be able to identify nest contents in order to get a better understanding of redpoll probability of nest survival.

Dunnocks in Waiman Bush had the same survivability during the incubation period as Kowhai Bush dunnocks. However, during the nestling period, dunnocks in Waiman Bush had lower survivability than in Kowhai Bush. This could be due to a low sample size of dunnocks at Waiman Bush. However, there was high mammalian predation on Waiman Bush dunnocks, and this predation occurred mainly during the nestling period. From the remains of the chicks, it seemed most likely that rats were the culprits of these depredation events. Rats are very difficult to control in mainland island projects due to their large numbers and reproductive rates (King 1990).

Dunnocks are very low nesters with most nests being at a maximum of one meter above the ground. It is possible that dunnock nests are more susceptible to rat predation than other species. A study by Moorhouse (1991) showed that there was very high rat predation on kaka nests that were within one meter of the ground. However, that does not explain why there would be higher survival of dunnock nestlings in Kowhai Bush since there is mammalian control occurring in Waiman Bush. It may be that there is a higher rat population in Waiman Bush than Kowhai Bush due to the mustelid trapping. Rats are prey for mustelids (King 1990; Murphy *et al.* 1998), and the removal of an important predator from a population can cause prey populations to increase (Innes *et al.* 1995). This is especially likely if the prey population, such as rats, are not controlled for to the same degree as the predator. Since there is intensive trapping occurring at Waiman Bush for mustelids it is probable for there to be a rat population that is increasing with their removal. Poison is distributed throughout the site for rat control; however not all rats will encounter the poison and some may not ingest a lethal dose (Innes *et al.* 1999). Therefore, it is possible for the rat population in Waiman Bush to be slightly higher than at Kowhai Bush, which could lead to some avian species having lower nest survival rates in Waiman Bush. However, it would be valuable to obtain larger sample sizes of Waiman dunnocks and carry out rat population counts in each study site to determine if this outcome was due to low sample number or differences in rat abundance.

Probability of Nest Survival in Native birds

When only mammalian predation is used for nest survival calculations, the majority of the native species in Waiman Bush had significantly higher survival rates than native species in Kowhai Bush. This shows that the mammalian predator control in Waiman Bush helped the nests of native species survive the breeding season.

Waiman Bush populations of brown creepers and grey warblers were two native species that were not well represented in this study. Many of these nests were too high to monitor, therefore it was not possible to get an accurate count of the egg or nestling exposure days. Larger sample sizes are recommended for these two species in order to get a more accurate view of their survival rates.

Egg and Nestling Survival

The probability of survival in each nesting stage was different among each study species. Some species had higher survival probabilities during incubation (e.g. brown creepers, fantails, grey warblers, blackbirds) while others have higher probabilities of survival during the nestling period (e.g. silvereyes and redpolls). There were also differences between the two study sites as to which species had higher survivability during incubation as compared to nestling period. For example, the redpolls and silvereyes in Kowhai Bush had higher survival during the nestling period, while Waiman Bush redpolls and silvereyes displayed no difference in survival between the nesting stages. This difference could be due to the difference in mammalian predator abundance between the two sites. Kowhai Bush has high mammal populations and it could be possible that there is higher predation during the incubation period because these nests could have been more conspicuous and easier to find. With more mammalian predators around, it may be difficult for Kowhai birds to find a safe nesting site that would deter these predators. However, Kowhai Bush dunnocks had higher survival probabilities for the incubation period than for the nestling period, as seen in their Waiman Bush counterparts. Dunnocks have very inconspicuous nests, and it is possible that they could elude predators of their location during the incubation period, but with increased visitation during the nestling period, this could lead potential predators to their nesting site.

Waiman Bush brown creepers had no difference in survival between the nesting periods, while brown creepers in Kowhai Bush had higher probabilities of survival during the nestling period than the incubation period. One possible explanation for this difference of nesting stage survival observed in the brown creeper population between the two study sites could be their evolutionary history. Native species evolved with avian predators that relied on vision to locate prey (Stevens *et al.* 1988); risk of avian predation could have induced this native species to build nests which were well concealed. In Kowhai Bush these perceivably well hidden nests helped them survive the incubation period, but increased activity during the nestling period could have been why there were higher predation rates during the nestling stage. However, further research is needed to

test if there are measurable differences in nest concealment between introduced and native species.

The majority of native species used in this study from Waiman Bush did not differ in survival between the two nesting stages. This could come from the previously described possibility of high rat populations. Rats use olfaction for predation (King 1990), which means that well hidden nests from vision may not deter these predators. It is possible that nests may be equally vulnerable in both nesting stages to predators which use olfaction.

The Kowhai introduced and native species populations had the same survival rate for the incubation and nestling period, while the Waiman introduced and native species populations had higher survival rates for the incubation period as compared to the nestling period. When introduced and native species survival probabilities were combined it was shown that there was no difference between survival in the incubation period and the nestling period in Kowhai birds, but in Waiman birds, there is a higher rate of survival during the incubation period than in the nestling period. Waiman Bush has less overall mammalian predator abundance than Kowhai Bush, which therefore could suggest that there are possibly more safe nesting sites available. There is less activity during the incubation period (Martin *et al.* 2000); therefore with very few mammalian predators many of the Waiman species would be able to escape predation during the incubation period. However, once the chicks are hatched there is increased activity at the nest. This increased activity could draw attention to the nesting site and it would be more likely for the few mammalian predators present to find their nest location.

Survival in Kowhai Bush and Waiman Bush

In Kowhai Bush the introduced species had a significantly higher rate of nest survival than the native species; however in Waiman Bush the introduced species had a significantly lower rate of nest survival than the native species. This shows that mammalian predator control is very beneficial to native bird populations. Introduced species did have increased nest survival rates in Waiman Bush as compared to Kowhai Bush, however not as high of an increase as was observed in the native species. Predator control at Waiman Bush increased the average nest survival of native species by over

30% (from 45.8% to 78.6% nest success), while introduced species only experienced an increase in nest success of about 10% (from 50.5% to 61.0%). As shown in these numbers, the native species survival rate was considerably boosted by the mammalian predator control. Introduced species rate of survival in Waiman Bush was also greater than in Kowhai Bush, but not nearly as great of a difference as displayed in the native species. This greatly increased rate of nest survival in native species with mammalian predator control shows how significant a threat introduced mammals are to the native New Zealand birds.

The results have shown that there was a higher rate of nest survival for birds in Waiman Bush as compared to Kowhai Bush. This illustrates that mammalian predator control projects are capable of increasing avian nest survival. Mammalian predator control is important for the ensured survival of many New Zealand bird species, and this study has shown that not only does mammalian predator control lower mammal populations, but it can also disproportionately increase native avian nest survival rates.

Although mammalian predator control has helped many bird species recover their numbers, there are some detrimental aspects to control methods. One concern is the prospect of secondary poisoning. This can occur if an insect or some other non-target animal ingests the poison. It is then possible for a bird to eat one of these insects and be harmed by the poison in the insect (Innes & Barker 1999). It is also possible that the birds themselves will ingest the poison and be harmed by the substance that is being used for their protection (Moorhouse *et al.* 2003). There are however, ways to deter birds from eating the poison. In aerial drops it is in sizes too big for the birds to eat. The poison is also dyed green and covered in cinnamon (Lloyd & McQueen 2000; Powlesland *et al.* 1999). Non-target trapping is also a concern. It is possible for birds to get caught in some of the traps, but measures are taken to keep these traps inaccessible to birds (Blair 2002).

Another concern with mammalian predator control, however, is possible prey switching (Jones 2003). Prey switching occurs when a predator's main prey is removed and the predator then switches to a new type of prey to substitute their diet (Murphy *et al.* 1998). Studies on the stomach contents of many introduced mammals has shown that birds do not seem to be the main prey, but that mice, rabbits, and insects are more favoured (Alterio & Moller 1997; Fitzgerald & Gibb 2001). However, if mice and rabbit

populations are reduced, predators then switch to New Zealand birds as their main prey type (Haselmayer & Jamieson 2001; Murphy *et al.* 1998). It is possible to avoid this situation if prey and predator populations are controlled at the same level, so that the prey population does not decrease faster than the predator population (Murphy *et al.* 1998). Even though there are some negative effects of mammalian predator control, with proper methods, it is possible to control for more than one predator species which can support the recovery of avian populations and the restoration of ecosystems (Saunders & Norton 2001). There must be careful planning when implementing predator control which includes careful assessment before and after control measures are taken (Courchamp *et al.* 2003). With careful planning, mammalian control can be beneficial to native species populations.

Conclusion

Introduced mammals are important nest predators on New Zealand birds (Duncan & Blackburn 2004). Native New Zealand birds did not evolve with mammalian predators (King 1984) and many seem to not realise that mammals are a threat. Upon the introduction of predatory mammals to New Zealand, many native bird populations decreased. The results of my study have shown that mammalian predator control can increase nest survival of common passerine species in New Zealand. Other studies have also shown that intense mammalian predator control during critical times during the avian lifecycle can help the survival of bird species (Kelly *et al.* 2005; Powesland *et al.* 1999). Increased nesting success was seen in kaka populations in areas with mammalian predator control (Moorhouse *et al.* 2003). Through the implementation of mainland island projects and offshore island eradication it is possible to facilitate native bird survival.

It is important to help native New Zealand birds recover from their lowered populations. However, this assistance comes in the form of changing the predator/prey dynamics by the removal of many mammalian predators and competitors. Studies have shown that birds are capable to responding to their relative risk of predation and changing their behaviours to decrease their risk of predation (Halupka 1998; Martin 1995; Martin & Ghalambor 1999). The native birds in New Zealand have been exposed to the majority

of the introduced mammalian predators for the past 200 years and to kiore for at least the past 1000 years (King 1984; Stevens *et al.* 1988). In that period of time, it could be possible that some of the native birds have come to recognise mammals as a potential threat and the removal of mammals from the breeding areas could cause changes in their life history strategies.

In the next chapter I compare the life history strategies of the introduced and native species in Kowhai and Waiman Bush. It will then be possible to see if the removal of mammals, as in mainland island projects and offshore island eradications, can cause life history strategies to change in the New Zealand avifauna.

Table 2.1. Probability of surviving (%) the entire nesting period for each species in Kowhai Bush (no predator control) and Waiman Bush (extensive predator control). The probabilities for survival included only mammalian caused failures. Number of nests given in parentheses.

Species	**Kowhai Bush**	**Waiman Bush**
Introduced species		
Song thrush	50.4 (200)	63.7 (89)
Redpoll	37.2 (61)	5.21 (8)
Dunnock	68.1 (32)	51.7 (11)
Blackbird	50.4 (94)	58.6 (44)
Native species		
Bellbird	36.9 (59)	90.4 (16)
Brown creeper	32.9 (26)	100 (9)
Fantail	74.9 (83)	79.2 (50)
Grey warbler	32.6 (63)	36.5 (10)
Silvereye	46.7 (88)	79.6 (11)

Table 2.2. Probability of nest survival (%) during the incubation and nestling periods in Kowhai Bush (no predator control) and Waiman Bush (predator control) for each study species. The calculations included only mammalian caused failures.

	Incubation period		**Nestling period**	
Species	**Kowhai**	**Waiman**	**Kowhai**	**Waiman**
Introduced species				
Song thrush	69.5	85.0	72.6	74.9
Redpoll	52.9	5.2	70.2	100
Dunnock	86.8	86.6	78.5	51.7
Blackbird	74.6	77.9	67.6	75.2
Native species				
Bellbird	63.5	90.4	58.1	100
Brown creeper	39.9	100	82.6	100
Fantail	88.0	94.7	85.1	83.6
Grey warbler	67.7	36.5	48.3	100
Silvereye	60.5	79.6	77.2	100

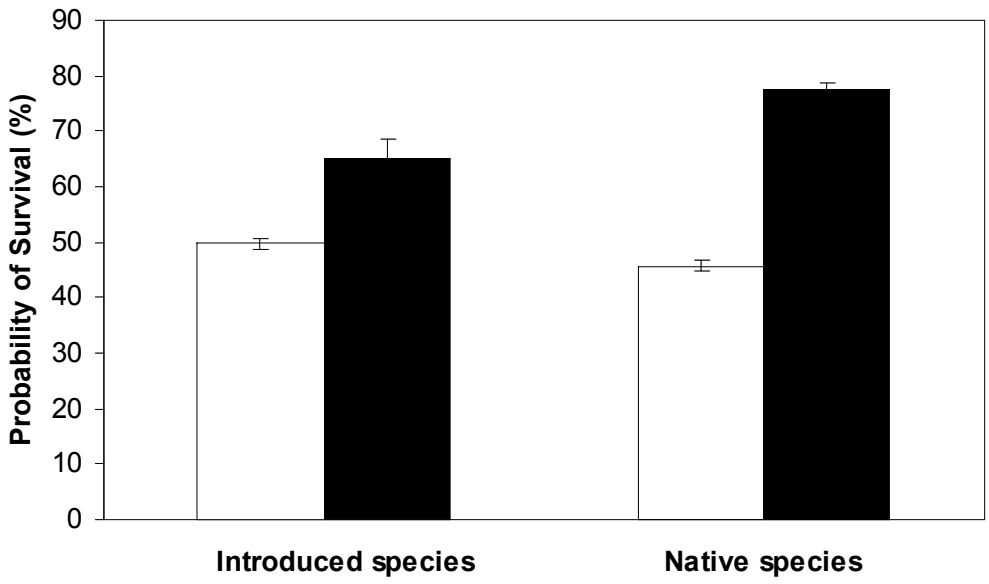

Figure 2.1. Overall probability of nest survival for all native and introduced species combined in both Kowhai Bush (no predator control; open bars) and Waiman Bush (predator control; black bars). Standard deviation is displayed.

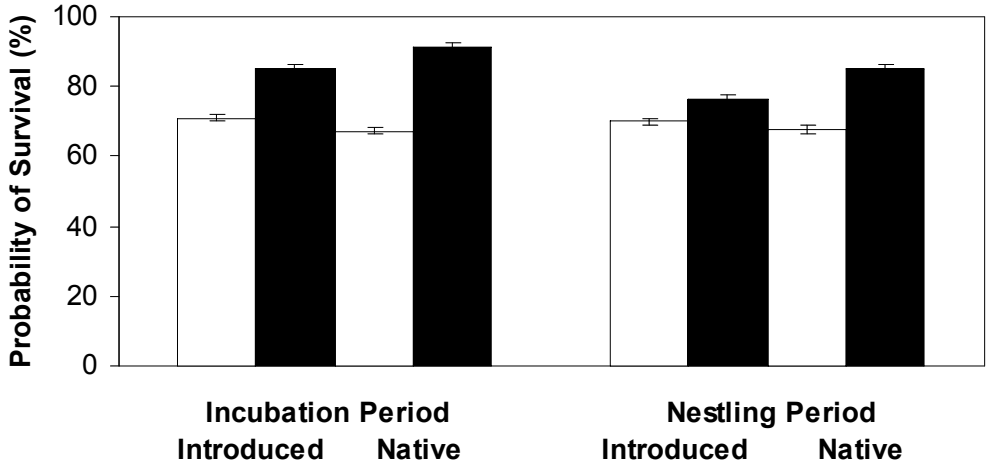

Figure 2.2. Nest survival of introduced and native species in Kowhai Bush (no predator control; open bars) and Waiman Bush (predator control; black bars) during the incubation and nestling periods calculated using only mammalian caused losses. Values are for all native species combined and for all introduced species combined within each study site. The standard deviation was calculated to show variation.

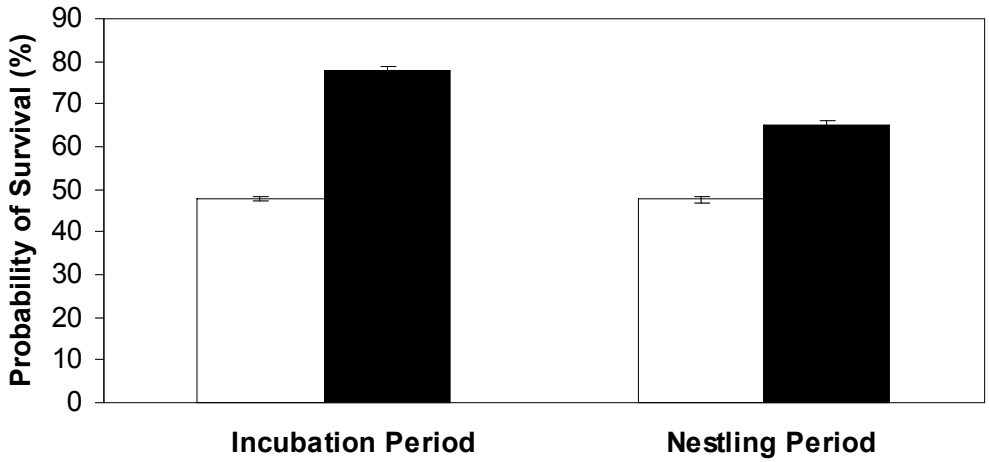

Figure 2.3. Probability of nest survival during the incubation and nestling periods for all species combined in both Kowhai Bush (no predator control; open bars) and Waiman Bush (predator control; black bars). The standard deviation was calculated.

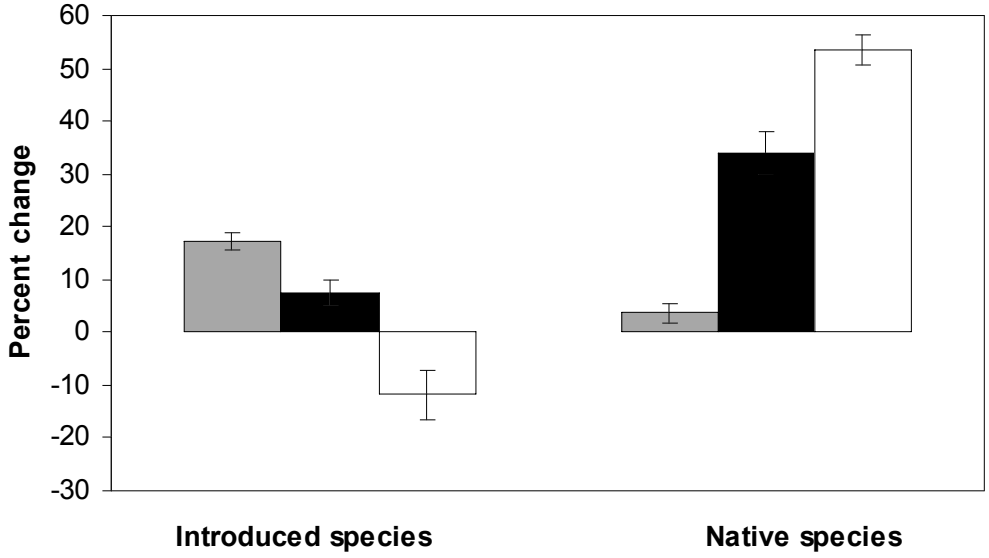

Figure 2.4. Percent change in nest survival between the two study sites. Introduced species (song thrush, grey bar; blackbird, black bar; and dunnock, white bar) change in nest survival from Kowhai Bush to Waiman Bush was compared with native species (fantail, grey bar; silvereye, black bar; and bellbird, white bar) percent change in nest survival. Calculations of the standard deviations are displayed. Positive values indicate that a species had higher nest success in Waiman Bush (predator control site) than in Kowhai Bush (little predator control).

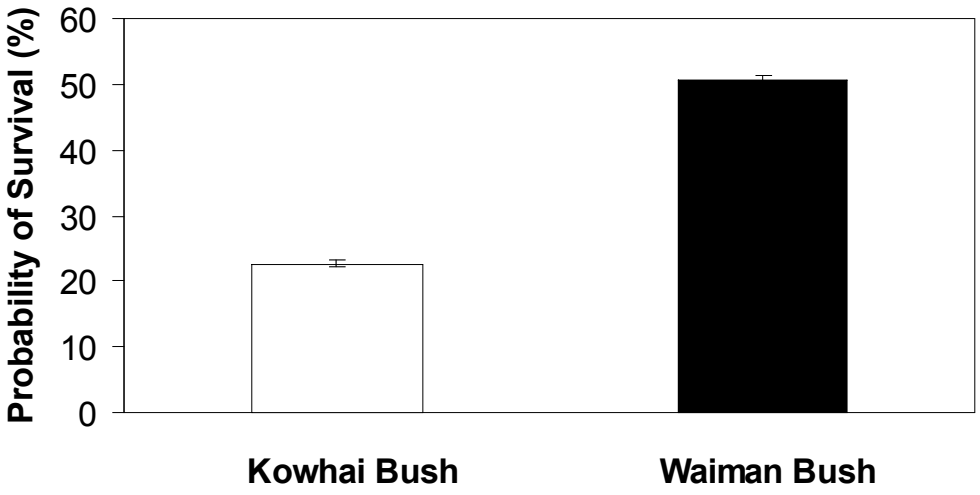

Figure 2.5. The total probability of nest survival for all species in Kowhai Bush (no predator control) and Waiman Bush (predator control). The survival probabilities were calculated using only mammalian caused failures. The standard deviation was calculated for each study site.

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Chapter 3

Plasticity of avian life history strategies in response to variation in nest predation risk

Abstract

Nest predation is a major cause of mortality in birds. On an evolutionary time scale, high rates of nest predation would be expected to select for changes in bird behaviour that minimize the risk of predation. Recent studies have found that birds are also capable of short-term changes (or "plasticity") in their reproductive behaviour due to local variation in predation risk. This study examined whether passerine birds in New Zealand (both native and introduced) can alter various aspects of their nesting behaviour when exposed to environments that vary in predation risk. This study was conducted at two native woodlands that differ in the risk of nest predation: one study site has intensive predator control while the other study site has little predator control. Both native and introduced birds showed rapid changes in their life history strategies in response to the differing risks of nest predation between the two study sites. Birds in the high risk study site had shorter nestling periods, higher incubation attentiveness, and lower visitation rates than the same species in an area where predators were controlled. Such changes should reduce the risk of nest predation by speeding up the time to fledging and reducing the likelihood of a predator locating a nest. My results suggest that birds are able to perceive the relative risks of nest predation and alter their behaviours in ways that increase the probability of nest survival.

Introduction

The avifauna of New Zealand evolved in the absence of mammalian predators (King 1984). This lead to many New Zealand bird species converging on various mammalian characteristics. For example, some became bigger, nocturnal, and even lost their ability to fly (Diamond 1981). The introduction of mammals to New Zealand caused many species to go extinct (Fleming 1962). The two recent waves of New Zealand avifaunal extinctions were due to the arrival of the Polynesians 1200 years ago, and the Europeans 200 years ago (Holdaway 1999; Stevens *et al.* 1988). Not only did humans prey on birds and cause their extinction, but they also brought many different species of mammals that also became predators (King 1984). Many life history characteristics of New Zealand birds, like flightlessness and low fecundity, made them vulnerable to introduced mammals (Duncan & Blackburn 2004). Furthermore, New Zealand birds did not possess the necessary defence mechanisms to deter mammalian predators.

The main predators on native New Zealand birds before the arrival of mammals were avian predators such as falcons (*Flaco novaeseelandiae*) and owls (*Ninox novaeseelandiae*); standing motionless and nesting under the cover of vegetation was enough to avoid such avian predators whose primary tool for prey location is sight (Gill & Martinson 1991). Research both in New Zealand and elsewhere in the world has shown that there can be a reduction in sensitivity to predators by species that did not co-evolve with predators (reviewed by Lima 1998 and Lima & Dill 1990). However, not all native New Zealand species went extinct with the arrival of predatory mammals, which leads to the hypothesis that the surviving New Zealand avifauna may possess some ability to change and adapt their life history strategies to increase survival in the presence of novel predators. In other words, native New Zealand birds may have a certain degree of behavioural plasticity that has allowed them to survive in the face of increased predation risk.

Differences in life history patterns that exist between populations of birds were initially thought to arise from differences in degrees of food limitation (Lack 1954; Martin 1987; Niethammer 1970). Skutch (1949) was one of the first researchers to argue that differences in life history strategies between populations could actually be the result of differences in predation risk. Recent research has also shown that variation in life

history traits are largely due to differences in predation risk (Briskie & Sealy 1989; Conway & Martin 2000; Ferretti *et al.* 2005; Lima 1987; Martin 1988; Martin 1995; Martin 2002; for a review of the food limitation vs. nest predation debate see Ricklefs 2000). Thus, nest predation can be a strong selective factor that can cause changes in bird behaviour (Franklin & Wilson 2003). However, to ensure survival it would also be beneficial for birds to respond rapidly (i.e., changes in individual behaviour rather than evolutionary changes over generations) to fluctuations in the level of nest predation risk. Such short-term changes in behaviour due to variance in predation risk are a type of behavioural plasticity (Ghalambor & Martin 2002). Plasticity in behaviour would allow birds to change certain aspects of their life history strategies in order to increase their overall fitness. As predation pressure changes continuously, anti-predator behaviour should be sensitive to the current level of predation risk (Rodd *et al.* 1997).

Nest predation is one of the main causes of mortality in birds (Ricklefs 1969); therefore the relative predation risk would be expected to influence many aspects of bird behaviour (reviewed by Lima 1998 and Lima & Dill 1990). Foraging and social behaviours of birds have been found to change with predation risk, which affects the amount of time spent looking for food (Barta *et al.* 2004; Caraco *et al.* 1980; Suhonen 1993), flocking behaviour (Beauchamp 2004; Krause & Ruxton 2002), and energy regulation (Koivula *et al.* 2002; Provasudov & Lucas 2001). Nest predation also greatly affects reproductive success of many bird species and can influence how much time eggs and offspring spend in the nest (Slagsvold 1982), where birds choose to nest (Bell 1983; Forstmeier & Weiss 2004; Roos & Pärt 2004; Ruxton & Humphries 2001; Stokes & Boersma 1998), the size of the nest (Antonov 2004; Møller 1990; Weidinger 2004), clutch size (Soler & Soler 1993), and parental visitation rates to the nest (Martin *et al.* 2000).

Low predation rate is correlated with higher hatching success (Rebergen *et al.* 1998), thus selection should favour birds capable of changing behaviours to increase nest survival. Some studies have found that nest predation rates are higher during incubation periods than in the nestling period because easy to find nests are preyed upon first in the early stages (Antonov 2004; Ricklefs 1969; Schaefer 2004). Therefore, inconspicuous nests have higher chances of survival through the nestling period (Ruxton & Humphries

2001). However, other studies have found higher nest predation during the nestling phase (Liebezeit & George 2002) due to increased noise by the begging nestlings (Redondo & Castro 1992; Skutch 1949) and visitation by parents during the nestling phase (Muchai & du Plessis 2005). Still, there are other researchers that have found no difference between daily survival rates in the incubation period as compared to the nestling period (Cresswell 1997; Farnsworth & Simons 1999; Schaefer *et al.* 2005). The discrepancy could be from different types of predators that are responsible for nest predation among the different studies (Schmidt & Whelan 2005). Visual predators might prey preferentially on poorly concealed nests while predators that use olfaction might focus on inconspicuous nests (Weidinger 2002). Nest predation is an important factor that has been shown to influence nest site (Lima 1993; Martin & Roper 1988; Stokes & Boersma 1998). It would be vital for individuals to be able to choose nest sites that lower nest predation risk (Amat & Masero 2004; Fernández & Reboreda 2002). However, it is difficult to predict nest success from individual nest variables (Filliater *et al.* 1994).

It has been hypothesised that in open nests clutch size should be reduced when predation risk is high (Doligez & Clobert 2003; Martin 1995). For some species there is a negative relationship between clutch size and the risk of predation (Eggers *et al.* 2006; Slagsvold 1982). Risk of nest predation could be directly related to clutch size since the time needed for feeding, incubation, and nestling period are all dependent on the number of eggs initially in the nest (Soler & Soler 1993). Furthermore, when there are more chicks the nest becomes noisier and could be more at risk for predation (Briskie *et al.* 1994; Skutch 1949). Thus, birds can incur more costs having a large brood compared to a small brood (Slagsvold 1984). Doligez & Clobert (2003) showed that clutch size in collared flycatchers (*Ficedula albicollis*) significantly decreased in years following high predation. Great tits (*Parus major*) have also been shown to decrease clutch size after a year of high predation, and their clutch sizes return to their initial values when predation risk is low for several years (Julliard *et al.*1997).

Niethammer (1970) discovered that introduced New Zealand species have smaller clutch sizes than their European counterparts. He suggested this could have resulted from the effects of a longer breeding season in New Zealand and possibly that these species have a longer life expectancy in New Zealand, although there is no data at present to test

this idea. With longer breeding periods and longer life expectancy, it is expected that clutch sizes will decrease. Recently, Congdon (2005) found that many introduced birds in New Zealand also lay smaller eggs than in their native range. Both results indicate that at least some life history traits (i.e., clutch size, egg size) have changed relatively rapidly since these species were introduced to New Zealand over a century ago, and that even more rapid changes in life history might be possible in relation to current variation in predation risk.

Predation risk can also influence the amount of activity that occurs around the nest (Eggers *et al.* 2005). Increased activity around the nest can increase nest predation risk as it alerts a potential predator to the location of the nest (Muchai & du Plessis 2005). Ghalambor & Martin (2002) found that when nest predation risk is high, an incubating parent will decrease feeding rates (i.e., decreasing the activity around the nest) and thereby increase nest attentiveness. Parental attentiveness can increase nest survival, especially if parents exhibit active nest defence (Cresswell 1997). Martin *et al.* (2000) showed that birds exhibit lower activity at the nest when there is high predation risk. Thus, predation is a strong selective factor that can decrease the amount of activity that occurs around the nest (Ghalambor & Martin 2000).

High risk of nest predation might also be expected to shorten incubation and nestling periods (Bosque & Bosque 1995; Martin 1995). Nest predation can influence the amount of time parents spend incubating the eggs (Eggers *et al.* 2005), resulting in a shorter incubation period. Shortened time in the nest could increase nest survival by decreasing the amount of time vulnerable eggs and chicks are exposed to nest predation. However, there is a threshold as to how quickly development can occur (Tieleman *et al.* 2004), but any shortening of time in the nest could potentially increase nesting success (Halupka 1998a). For example, rhinoceros auklet (*Cerorhinca monocerata*) chicks fledge younger and at lower body mass in areas with high predation (Harfenist & Ydenberg 1995). This occurs because parents stop feeding the chicks earlier in high-risk areas to induce the chicks to fledge sooner. However, it is not known whether or not the chicks suffer higher mortality rates when forced to fledge early. Nevertheless, a study by Yamaguchi & Higuchi (2005) showed that the nestling period of the varied tit (*Parus varius owstoni*) also decreases when there is high nestling predation.

Moors (1983) compared predation rates of eggs and chicks between introduced and native New Zealand birds. His study found no difference between the predation rates, but using a larger data set I found that native birds generally experienced higher rates of nest predation than introduced species in areas with no predator control (chapter 2). Native birds may not be able to cope with high predation rates by introduced mammals compared to introduced species that evolved with mammals because of different life history traits. Trevelyan & Read (1989) tried to determine if New Zealand birds differ from their continental relatives in Australia (where birds did evolve with mammals) by comparing differences between the two populations in incubation and nestling periods. However, even though Australian birds were predicted to have different life history strategies compared to New Zealand birds, no significant differences were found. They suggested this could be due to the high selective pressure from the introduced mammals on New Zealand birds, which has caused the New Zealand birds to acquire life history strategies like Australian birds thereby increasing their chances of survival. These changes would have occurred over the last 1200 years; the time when mammals were first introduced to New Zealand. However, it is possible for changes in life history strategies to occur within decades instead of thousands of years when there are high selection pressures (van Noordwijk *et al.* 1980). It is not known how fast life history strategies can change (Trevelyan & Read 1989); this study attempts to see if changes in life history strategies, due to variation in predation risk, can occur within just a few years.

The aim of this chapter is to determine to what extent New Zealand birds exhibit behavioural plasticity in life history strategies, and to determine if such changes can occur within a few years. A variety of life history traits were compared between native and introduced species in an area where predators had been recently removed (thus decreasing the risk of nest predation), with a control area with little predator removal. I also determined if there was a difference between native and introduced birds in the extent to which they changed their life history strategies due to the different evolutionary backgrounds that introduced birds have had with mammalian predators. It is likely that the introduced birds are more capable of assessing their relative risk of predation and altering their behaviours to increase their chances of survival.

Methods

Study sites

A description of the study sites are given in Chapter 2. This included both Kowhai Bush, an area with little predator control, and Waiman Bush, an area with extensive control of rats (*Rattus norvegicus, R. exulans,* and *R. rattus*), cats (*Felis catus*) and mustelids (*Mustela furo, M. erminea,* and *M. nivalis*).

Introduced Birds

The introduced species used in this study included blackbirds (*Turdus merula*), song thrushes (*T. philomelos*), redpolls (*Carduelis flammea*), and dunnocks (*Prunella modularis*). Blackbirds are abundant in both the North and South Island and feed on worms and fruit. Their breeding season is from July to January. The average clutch size is 2-4 eggs. Song thrushes are common within New Zealand and feed on snails, worms, insects, berries, and fruit. Their breeding season is from June to January and they lay clutches containing 3-5 eggs. Redpolls are distributed throughout New Zealand, but are more common on the South Island. They feed on insects, seeds, and plants. The breeding season is from September to January with clutches containing 4-5 eggs. Dunnocks are dispersed widely in New Zealand and feed on insects and seeds. Their breeding season is from August to January. Dunnock nests are usually close to the ground and contain 3-5 eggs per clutch (Kinsky & Robertson 1987). The introduced species used in this study were equally abundant in both Kowhai Bush and Waiman Bush.

Native Birds

The native species used in this study included fantails (*Rhipidura fuliginosa*), bellbirds (*Anthornis melanura*), silvereyes (*Zosterops lateralis*), grey warblers (*Gerygone igata*), and brown creepers (*Finschia novaeseelandiae*). Fantails can be found abundantly on both the North and South Island. They reside in habitats with trees and shrubs and commonly feed on insects. Their breeding season is from August to January. The average clutch size is 3-5 eggs. Bellbirds are abundant on the South Island but are rarely found north of Auckland. They feed on nectar, insects, and fruit. The breeding season is from

September to January with clutch sizes of 3-4 eggs. Silvereyes are common in the North and South Island including subalpine areas. Common food includes insects, nectar, berries, and fruit. Their breeding season is from August to February. Clutch sizes range from 2-4 eggs. Grey warblers are common within New Zealand and feed on spiders and insects. The breeding season is from August to December with average clutch sizes of 3-5 eggs. Brown creepers are only located on the South Island. They feed on insects, moths, and grubs. Breeding occurs from November to January and have clutch sizes of 3-4 eggs (Kinsky & Robertson 1987; Soper 1976; Stead 1932). The native species examined in this study are regularly found in both sites.

Data collection

Nests were located by following adult birds carrying nesting material or food to the nest or by systematically searching the vegetation in areas of preferred habitat (methods for finding and following nests was adopted from Martin & Geupel 1993). Once nests were found a small amount of flagging tape was used for relocation. The tape was placed in an inconspicuous spot and at least 3m away from the nest to keep predators from locating marked nests. However, previous studies have found that there is no difference in predation between marked and unmarked nests (Nilsson *et al*. 1985) nor did the distance of the marker from the nest have an impact on predation rate (O'Reilly & Hannon 1988). Long poles with mirrors attached to the end were used to view the contents of nests situated high in the canopy. The status of each nest was recorded during each visit.

If the nest was empty when found it was visited daily in order to establish the date the first egg was laid. If the nest was found containing eggs the nest was visited the next day. If a new egg was found in the nest it was visited daily until laying was complete. When laying was complete, the clutch size could be determined. Once incubation began the nest was visited every two or three days to determine if the nest had been depredated. A nest found with a newly hatched chick and eggs was visited the next day to establish how many eggs hatched. When all chicks had hatched the nests were visited every two to three days until the chicks fledged or the nest was depredated. Regularly approaching the nest does not have an impact on predation rate (Farnsworth & Simons 1999; Keedwell &

Sanders 2002; Mayer-Gross *et al.* 1997; Verboven *et al.* 2001). It has been shown that daily visits to the nest can decrease hatching success (Blackmer *et al.* 2004). However, this was shown to be the case in very long-lived birds that were naïve to investigators and were disturbed everyday until hatching. In our study the species are short-lived and visitation did not occur daily throughout the entire nesting period. Nevertheless, to decrease any risk of increased predation on visitation rate, daily visits were not conducted over the entire nesting period and damage to nests and the surrounding area was minimized (Major 1990). Nests in both study areas were visited in the same way, so any effect of nest visitation should be similar.

Incubation period was defined as the time from the day the last egg was laid to when it hatched. The nestling period was defined as the time between the day the first chick hatched to when it fledged. A nest was determined to have fledged if the chicks were seen fledging or if a nest was found empty (with no signs of predation) and the nestlings were ready to fledge the previous day. Predation was concluded if eggs were missing, egg shells were present in the nest, the nest was damaged in some way, or if chicks were gone before they were ready to fledge. Chicks that were dead in the nest were examined for sign of predation. Peck marks on the chicks were most likely caused by the shinning cuckoo. If there was no obvious predation sign on the young they were determined to have starved or drowned as can occur with heavy rainfall.

Video recordings were used to monitor adult incubation attentiveness and the number of visits the parents made to and from the nest. I set up cameras (Sony Hi8 Handycams) from 5 to 15 m from the nest. Cameras were set up within the first hour of sunrise and filming continued for up to six consecutive hours. Nests were filmed during both the incubation period and nestling period. Filming at nests during incubation occurred at least five days after the last egg was laid and nestlings were video taped at the point when their primary feathers began to break from their sheath (1-2mm). This ensured that the parents were observed in normal incubation behaviour and that all nestlings video taped were at the same stage of development since many different species were used in this study. Some of the video camera tapings during the incubation period induced desertion of eggs; it is not known why this occurred although in some cases the camera may have been too close. These nests were not included in the analysis. The

presence of cameras has not been found to increase predation rate on nests or effect nest survival (Keedwell & Sanders 2002; Sanders & Maloney 2002; Stake & Cimprich 2003). After filming tapes were transcribed in the lab. Adult nest visitation was calculated as the number of visits to the nest per hour. Nest attentiveness was determined by calculating the percent of time the parents spent on their eggs during the filming.

Analysis

Clutch size, length of incubation period, length of nestling period, incubation attentiveness, nest visitation during the incubation period and visitation during the nestling period were compared between each species in the two study sites. Thus, my study has a paired design in which I compared the life history traits of one species in Waiman Bush (predator control) with the same species in Kowhai Bush (no predator control). This was then repeated for each species, both native and introduced. I used a total of 642 nests for my clutch size analysis. For the incubation period there were 162 nests used. There were 213 nests used for the nestling period analysis. Sample sizes were smaller for both these measures as nests were often found after laying was finished or were depredated before hatching or fledging. Data on visitation rates during the incubation period and incubation attentiveness were taken from 213 nests filmed in both sites. Visitation rates during the nestling period were taken from 142 nests filmed. I used multifactor ANOVA on each life history strategy to determine whether variation in a particular life history trait (e.g. visitation rate) was due to species, study site (predator control vs. no predator control) and origin of species (native vs. introduced). The observed life history trait was the response variable with study site, origin of species (introduced or native), species, and year as factors. All data were normally distributed. The program R was used for the analysis. Year was significant only for incubation visitation thus all data were combined over years as sample sizes of individual species in each year were too small to analyse years separately or to exclude years. Species which had the largest sample sizes were included in the figures. As shown in chapter 2, there were significant differences in nest survival rates between the two study sites.

Results

Clutch size

Clutch size did not differ significantly between the two study sites (Figure 3.1; $F_{1,640} = 0.24$, $p = 0.63$). There was a slight difference in clutch size between introduced and native species ($F_{1,639} = 3.71$, $p = 0.054$) and a significant difference in clutch size between individual species ($F_{7,632} = 3.23$, $p = 0.0020$). However, the overall interaction of site and origin did not differ significantly ($F_{1,628} = 0.30$, $p = 0.58$) nor did the interaction of origin and species ($F_{7,621} = 0.10$, $p = 0.99$).

Incubation period

The incubation period was not significantly different between sites (Figure 3.2; $F_{1,160} = 0.18$, $p = 0.68$), origin ($F_{1,159} = 1.59$, $p = 0.21$), the interaction of site and origin ($F_{1,148} = 0.0033$), or the interaction of site and species ($F_{3,145} = 0.98$, $p = 0.98$). However there was a significant difference between the incubation periods of individual species ($F_{7,152} = 5.07$, $p < 0.00001$).

Nestling period

There was a significant difference in the length of the nestling period between the two sites ($F_{1,211} = 17.06$, $p < 0.0001$). Nestling periods in Waiman Bush were significantly longer than in Kowhai Bush (Figure 3.3). For example, both blackbirds and fantails had significantly longer nestlings periods in Waiman Bush compared to Kowhai Bush. There were also differences in length of nestling period observed among individual species ($F_{7,203} = 4.42$, $p < 0.0001$). However, there was no significant difference between introduced and native species ($F_{1,210} = 1.58$, $p = 0.21$), the interaction of site and origin ($F_{1,199} = 1.89$, $p = 0.17$), or the interaction of site and the length of nestling period in each species ($F_{4,195} = 0.24$, $p = 0.91$).

Visits during incubation

Parental visitation during the incubation stage was significantly different between the two sites ($F_{1,211} = 6.67$, $p = 0.011$). Parents visited the nest significantly more in

Waiman Bush than in Kowhai Bush (Figure 3.4). There were also significant differences in visitation rates between introduced and native species ($F_{1,210} = 83.31$, $p < 0.000001$), as well as between species ($F_{7,203} = 11.73$, $p < 0.000001$). However, there was no difference in the interaction of site and origin ($F_{1,198} = 0.066$, $p = 0.79$), or the interaction of site and species ($F_{6,192} = 1.27$, $p = 0.27$).

Incubation attentiveness

The percent of time the adults sat on their eggs during the incubation period did not differ significantly between the two sites ($F_{1,211} = 0.031$, $p = 0.86$), or in the interaction of site with origin ($F_{1,198} = 1.79$, $p = 0.18$). Conversely, there was a significant difference in incubation attentiveness between introduced and native species ($F_{1,210} = 250.98$, $p < 0.000001$), individual species ($F_{7,203} = 76.27$, $p < 0.000001$), and the interaction of site and species ($F_{6,192} = 3.26$, $p = 0.0045$). Individual species, such as the song thrush and bellbird in Waiman Bush had lower nest attentiveness than their Kowhai Bush counterparts (Figure 3.5).

Nestling visitation

Parental visitation during the nestling period differed significantly between the two sites (Figure 3.6; $F_{1,140} = 4.28$, $p = 0.041$). Birds in Waiman Bush had significantly more visits per hour to their nests than did the same species in Kowhai Bush. There was also significant differences in visitation rate between introduced and natives ($F_{1,139} = 251.85$, $p < 0.000001$), and between individual species ($F_{7,132} = 12.88$, $p < 0.000001$). There was no difference in nestling visitation rate observed in the interaction of site and origin ($F_{1,127} = 0.032$, $p = 0.86$), or in the interaction of site and species ($F_{5,122} = 0.84$, $p = 0.52$).

Discussion

I found that a variety of life history traits differed between my study site at Kowhai Bush (an area with little predator control) and at Waiman Bush (an area with extensive predator control). Although I found no differences in clutch size or the length of the incubation period between the two sites, I did find that birds nesting in the site with

few predators changed their behaviours in such a way that they increased the length of the nestling period, decreased nest attentiveness, and increased nest visitation in most species. These changes are all the more remarkable in that they have not developed over evolutionary time, but rather in the space of only a few years from the time predator control was initiated at the Waiman Bush study site. The directions of these changes are exactly what one would expect of birds in more risky sites. Life history theory suggests that high nest predation risk should cause changes in the behaviour of birds and that they should adjust their life history traits in such a way so as to reduce the probability their nests fall victim to predators. Both native and introduced species in my study appeared to be plastic in their responses as both groups of species altered their life history traits in response to the differences in predation risk between the two study sites.

Clutch size

Previous studies have found that when there is low risk of nest predation clutch size will increase (Ferretti *et al.* 2005; Slagsvold 1982). However, in this study clutch size did not change when the risk of nest predation was reduced. There were differences in clutch size observed between introduced and native species as well as between species. This is to be expected, because different species have different life history strategies. However, these differences did not correspond to the change in nest predation risk when predators were removed in Waiman Bush. There was no difference in overall clutch size between Waiman Bush and Kowhai Bush. This could arise from the short time frame in which the decreased nest predation risk was observed. Yet, others researchers have found that clutch size was decreased in the year following increased nest predation risk (Doligez & Clobert 2003; Julliard *et al.* 1997). At present, I have no explanation for why clutch size did not change in my study.

A recent study by Fontaine & Martin (2006) observed results similar to this study relating to clutch size. When nest predation risk was lowered there was no change in average clutch size. Even though clutch size did not change they did discover that there was an increase in egg mass and clutch mass when nest predation was lowered. An increase in clutch size would incur higher investment for the parents (Slagsvold 1984), whereas an increase in egg mass and clutch mass is beneficial to the developing embryos

by providing extra nutrients, but most likely does not have as much impact on parents as an increase in clutch size. Sockman (1997) found that brood size does not impact the risk of nest predation; therefore clutch size may not change with nest predation risk. Future studies of introduced and native birds in New Zealand could include measures of egg mass and clutch mass at these two study sites to see if there are changes when nest predation risk is lowered, as has been observed by other studies. A recent study by Congdon (2005) found that many introduced species in New Zealand had smaller egg sizes than in their native range in the United Kingdom, confirming egg size could be a plastic trait. A comparison of egg size between my study sites would be useful to determine if birds are changing egg size rather than clutch size and thereby taking advantage of the decreased nest predation risk without incurring as high a cost to themselves. This could more accurately measure plasticity and egg investment differences between introduced and native birds.

Incubation period

This study observed significant differences between the length of incubation period in individual species, however there was no differences due to changes in predation risk. With decreased nest predation risk the incubation period did not change between the two study sites. This does not support the hypothesis that decreased risk of nest predation will cause an increase in the incubation period. The lack of change in the length of the incubation period could be the result of developmental constraints of the growing embryo (Tieleman *et al.* 2004). It may not be possible to significantly change the time the developing embryo spends in the egg. Therefore, this life history strategy may not be as plastic as other behaviours due to physiological limitations. However, the decrease in incubation attentiveness in the predator control area would suggest a flow-on effect to the length of the incubation period. As sample sizes were small for some of my study species it would be worth continuing this aspect of the study to determine whether changes in incubation patterns do affect the length of the incubation period, and if not, why birds spend more time on the nest in areas with more predators.

Nestling period

When nest predation risk was decreased there was an increase in the length of the nestling period. The nestling period was significantly longer in Waiman Bush as compared to Kowhai Bush. When nest predation risk is lowered it may be beneficial for chicks to stay longer in the nest. This could occur if chicks will be more developed and stronger when they fledge. In Kowhai Bush, where the nest predation risk is higher, parents might encourage their chicks to fledge as soon as possible to decrease their chances of being depredated in the nest. However, in Waiman Bush where nest predation risk is lower, parents have the option of keeping their chicks in the nest for a longer period of time. Other studies have also found that nest predation risk can cause changes in nestling period (Bosque & Bosque 1995; Halupka 1998a; Halupka 1998b; Martin 1995; Remeš & Martin 2002; Yamaguchi & Higuchi 2005). This shows that parents are capable of assessing the relative risk of nest predation and benefit by delaying chick fledging when nest predation risk is low. There was no difference in the flexibility of introduced or native species with regards to the nestling period, which shows that not only are introduced species plastic in this life history strategy, but also the native species used in this study will also increase the length of the nestling period when nest predation risk is lowered.

Visits during incubation

Incubation visitation rates were higher when nest predation was decreased. Parents in Waiman Bush visited their eggs more frequently and thereby increased activity at the nest when nest predation risk was lowered. Other research has also observed that there is increased nest activity when nest predation is lowered (Conway & Martin 2000; Ferretti *et al.* 2005; Ghalambor & Martin 2000). Parents visit the nest more when there is less chance of being spotted by a predator. The interaction of site and origin was not significant in this study, which shows that introduced and native species did not differ in the extent to which they changed their incubation visitation. This shows that the introduced and native New Zealand species in this study are equally plastic in this life history strategy. This runs counter to the hypothesis that introduced species will increase activity at the nest when nest predation risk is lowered while native species will not. The

resulting outcome was not expected because of the differing evolutionary histories of native and introduced species with mammalian predators.

Incubation attentiveness

While this study did not find an overall difference between the two sites in incubation attentiveness when nest predation was decreased, there was a difference between how individual species changed between sites. This may be due to some species being more plastic in this behaviour than other species. There was no significant difference between the interaction of site and origin which shows that native and introduced species in the two sites changed this behaviour to the same extent. However, there was a difference observed in the site and species interaction. Individual species in Waiman Bush spent less time on their eggs compared to their Kowhai counterparts. For example, both bellbirds and song thrushes in Waiman Bush had lower incubation attentiveness compared to their Kowhai counterparts. This shows that the plasticity of incubation attentiveness exists at the species level, which may result from species differences in vulnerability to predators.

It would be beneficial for species that are more vulnerable to nest predation risk to be able to change the amount of time spent on their eggs which changes the amount of activity at the nest. Increased nest attentiveness decreases the amount of activity to and from the nest, therefore when nest predation risk is high species should increase nest attentiveness to decrease nest activity (Ghalambor & Martin 2002). However, there may be differences in nest predation risk among individual species which would cause incubation attentiveness to change in some species and not in others. There could be differences in the ability of individual species to mount an effective nest defence and this could alter the benefits of increased attentiveness. In species that have active nest defence against predators, it would be beneficial to spend more time at the nest to defend the contents, thereby increasing nest attentiveness (Verboven *et al.*2001). The differences in incubation attentiveness between species could also result from some species being more flexible in this behaviour than others. While there was no overall difference in incubation attentiveness between the two sites in this study there was a difference seen at the species level between the two sites.

Nestling visitation

Parental visits to the nest during the nestling period increased significantly when risk of nest predation was decreased. Waiman Bush birds had higher activity at the nest as compared to Kowhai Bush birds, which is most likely due to the lower nest predation risk at Waiman Bush. Previous research has shown that birds with high risk of nest predation will decrease the amount of activity that occurs at the nest by decreasing parental nest visitation (Eggers *et al.* 2005). There was no difference in the interaction of site and origin, which suggests that introduced and native species are both changing their visitation rate in a similar manner between the two sites. This demonstrates that the native species used in this study are capable of changing their nest visitation rate when there is a change in the risk of nest predation, which rejects the hypothesis that native species are less plastic in visitation rate than introduced species.

As clutch size did not change between my two study sites, but yet visitation rates decreased, parents must somehow compensate for less frequent visits to meet a similar demand. In other words, if parents are feeding four chicks in both study areas, how do the birds in Kowhai Bush, with lower visit rates, manage to feed the same number of chicks? One possibility is that parents compensate for reduced feeding visits by bringing more food with each visit. I recorded the number of chicks fed during each visit to try to assess if this was occurring, but my sample sizes were too small to test for any differences. It would be interesting to continue this work in the future to determine exactly how parents trade off changes in one life history trait with that of another.

Conclusion

The arrival of predatory mammals to New Zealand was detrimental to many of the native avifauna (Gill & Martinson 1991), however not all species were harmed. Bellbirds still have a relatively large distribution around the country (Kelly *et al.* 2005). This suggests that some native species may be more adaptable to changing conditions than others. Some native species may possess plasticity in their life history strategies, which would be beneficial for survival.

This study has shown that some life history strategies are more plastic than others in regards to nest predation risk. For example nestling period, incubation visitation,

incubation attentiveness, and nestling visitation readily changed in response to changing predation risk and were relatively plastic, while clutch size and incubation period did not change when risk of nest predation changed. I also found that introduced species were not more plastic in their life history strategies than native species. Native species in this study showed changes in their life history strategies similar to the introduced species studied. Native birds are showing an ability to adapt to exotic predators in ways that reduce nest predation risk. Furthermore, the life history strategies in this study were observed to change in just three years. This shows how readily birds can assess their risk of nest predation and that life history strategies are capable of changing in a short period of time.

Future studies in New Zealand could look to see if there are differences in persistence between introduced and native birds. Roper (2005) found that breeding persistence may be a more important factor for differences in evolutionary processes between temperate and tropical passerine birds than predation avoidance. Birds may increase nesting survival by being able to renest faster. Native New Zealand birds may have less breeding persistence than introduced birds due to differences in their evolutionary histories. It would also be interesting for future research to compare life history traits of native mainland birds with native birds that are only capable of surviving on predator free offshore islands (e.g. saddlebacks (*Philesturnus carunculatus rufusater* and *P.c.carunculatus*), stichbirds (*Notiomystis cincta*), and black robins (*Petroica traversi*)).

It would also be beneficial to see if there are differences in nestling begging calls between native and introduced species. Nest predation can cause variation in nestling begging calls. Species that are subject to high nest predation have evolved begging calls that decrease their detectability to predators (Briskie *et al.* 1999). Begging calls of native and introduced New Zealand birds could be compared between areas with high predation to areas with low predation to determine if begging calls have any plastic attributes.

The results of this study have shown that the removal of mammalian predators in New Zealand habitats can cause changes in introduced and native avian life history strategies. This has implications for conservation managers because birds may become less sensitive to mammalian predators with their removal. If birds do become less responsive to mammalian predators when their populations are reduced then conservation

measures of mammal control must be continued in order to protect native species. The next chapter examines whether there are differences in response to a potential mammalian predator between the two study sites to see if birds do become less sensitive to predators upon their removal.

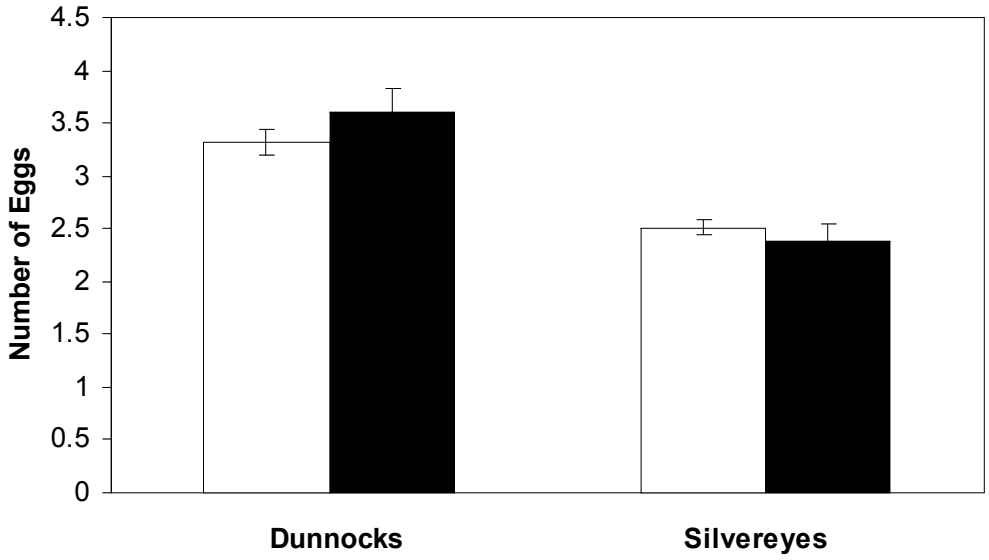

Figure 3.1. Example of changes in the average clutch size for two species in the study. Neither dunnocks nor silvereyes had significantly different clutch sizes between the study area in Kowhai Bush (little predator control; open bars) and Waiman Bush (extensive predator control; black bars). Standard errors are shown. All other species examined also showed no significant difference in clutch size between the two study sites.

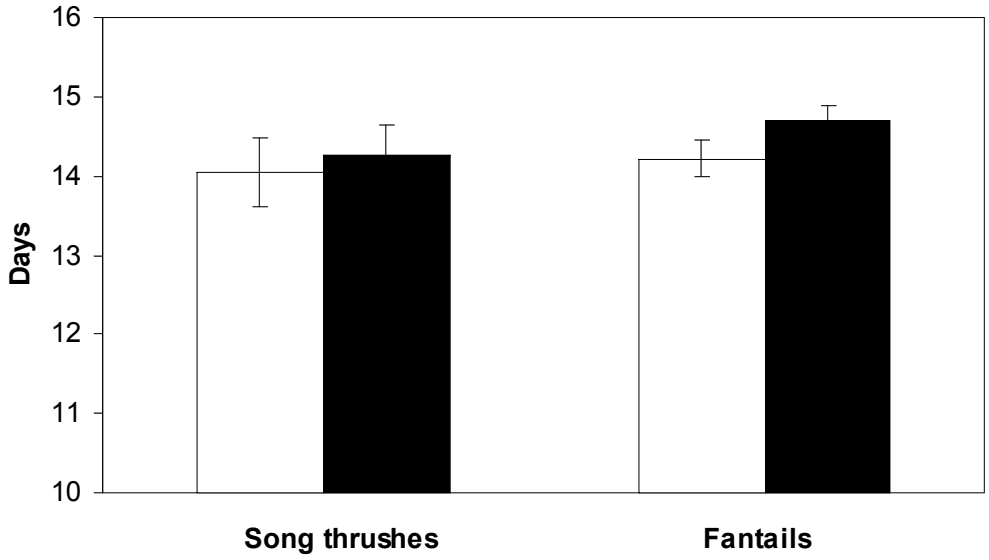

Figure 3.2. Examples of change in the length of the incubation period for two species in Kowhai Bush (little predator control; open bars) and Waiman Bush (extensive predator control; black bars). There was no significant change for either song thrushes or fantails, or any of the other species studied. Standard errors are shown.

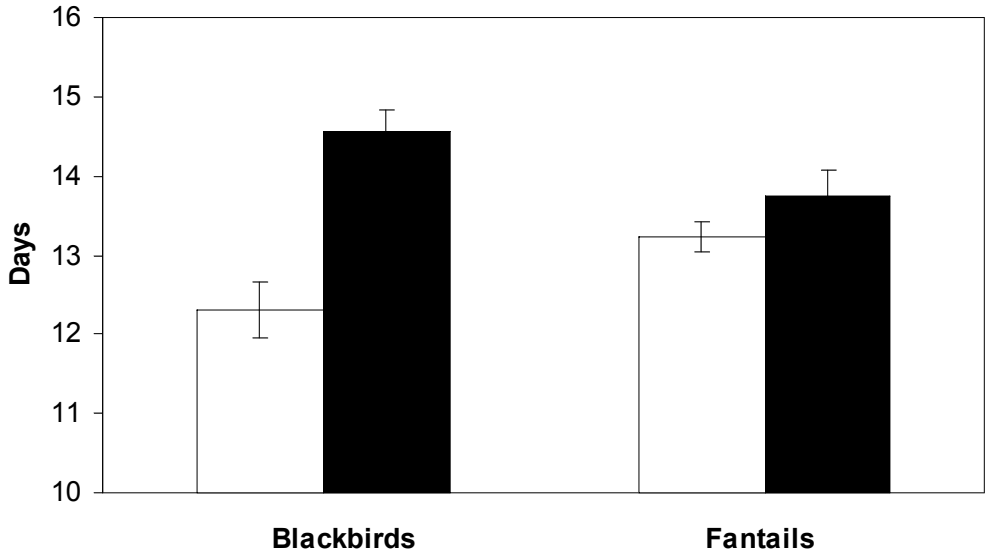

Figure 3.3. Changes in the length of the nestling period of blackbirds and fantails in Kowhai Bush (little predator control; open bars) and Waiman Bush (extensive predator control; black bars). Both species had significantly longer nestling periods in the areas with predator control. Other species showed a similar pattern where sample sizes were large enough to carry out a statistical comparison. Standard errors are shown.

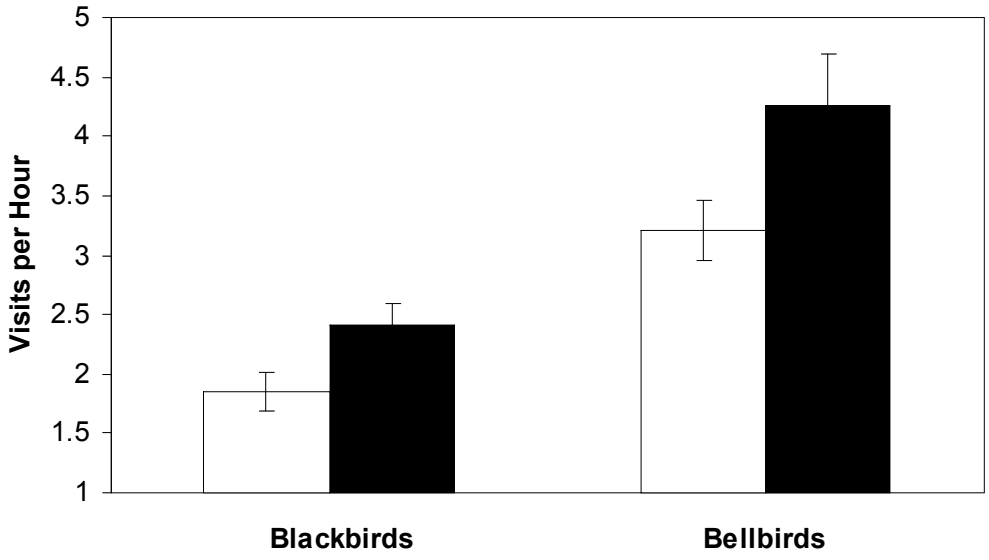

Figure 3.4. Rates of visits to the nest by blackbird and bellbird parents during the incubation period for birds in Kowhai Bush (little predator control; open bars) and Waiman Bush (extensive predator control; black bars). In both species the rates of visits to the nest increased in the area with greater predator control. Other species showed a similar pattern although sample sizes were too small to allow a statistical comparison. Standard errors are shown.

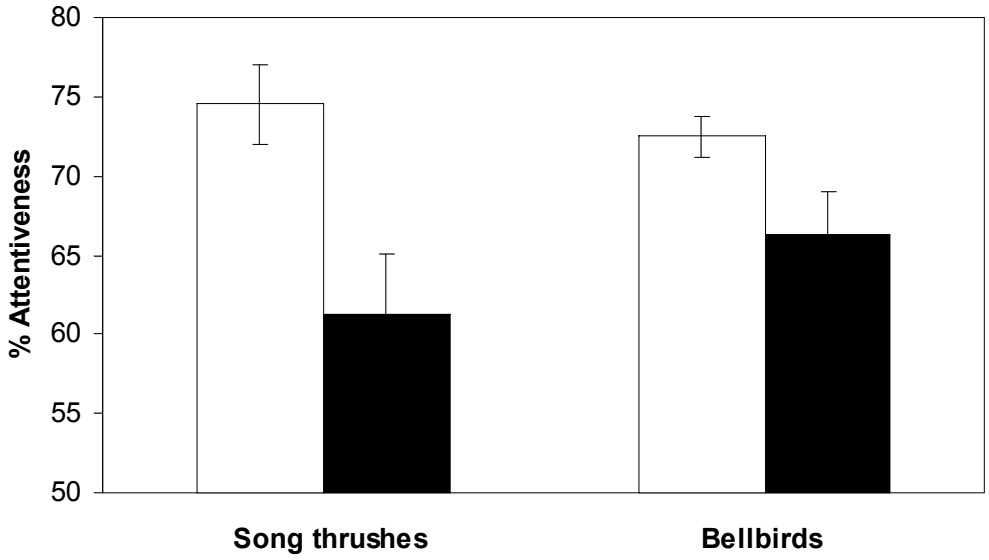

Figure 3.5. The percent of time parents spend during the day sitting on their eggs (defined as percent attentiveness) for song thrushes and bellbirds in Kowhai Bush (little predator control; open bars) and Waiman Bush (extensive predator control; black bars). In both species, adult nest attentiveness decreased in the area with extensive predator control. Other species showed a similar pattern although sample sizes were too small to allow a statistical comparison. Standard error is shown.

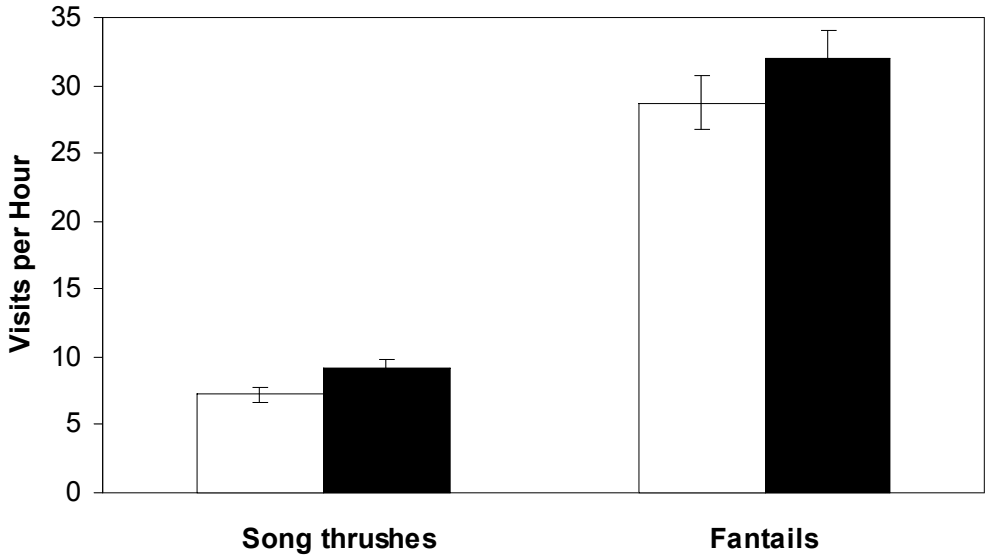

Figure 3.6. Rates of visits to the nest by song thrush and fantail parents during the nestling period for birds in Kowhai Bush (little predator control; open bars) and Waiman Bush (extensive predator control; black bars). In both species the rates of visits to the nest to feed nestlings increased in the area with greater predator control. Other species showed a similar pattern although sample sizes were too small to allow a statistical comparison. Standard errors are shown.

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Chapter 4

Differences in the response of native and introduced birds to an experimental nest predator in areas with differing risks of predation

Abstract

Conservation in New Zealand generally focuses on the removal of introduced mammalian predators. Removal of introduced predators is particularly important for the continued survival of many native New Zealand birds. Previous studies (including this one; see chapter 3) have shown that birds can change their life history strategies when predators are removed; however, it is not known if birds become less sensitive to predators when the risk of predation is lowered through predator control measures. In this study I tested whether the removal of introduced predators has changed the response of the native grey fantail (*Rhipidura fuliginosa*) and the introduced song thrush (*Turdus philomelos*) to the experimental presentation of a cat model at their nests. The study was carried out in two study sites where one site had little mammalian predator control and the other had rigorous mammalian predator control. There was no change in adult incubation behaviour in either species between the sites. Birds did not display changes in response to the presentation of the cat at their nests when the model was removed. However, during the nestling stage, both fantails and song thrushes in the predator control site increased their rate of visitation after the presentation of the model. This result was opposite to that expected and may be due to overall changes in adult investment strategies when mammalian predators are removed. Alarm calling by song thrushes was significantly less frequent in the area with predator control, and birds were more likely to return to their nests than in areas with little predator control. Birds seemed to have lost the ability to recognise mammals as a threat when mammals were removed from their environment.

Introduction

Nest predation is a major cause of mortality in birds (Ricklefs 1969). As a consequence, nest predation can be a strong selective factor and can affect the evolution of avian life history strategies (Franklin & Wilson 2003). However, it has recently been shown that birds are capable of monitoring their relative risk of predation and can modify their behaviours to reduce this risk (Ghalambor & Martin 2002; Halupka 1998; Julliard *et al.* 1997; Koivula *et al.* 2002; Lima 1998; Martin 2002; Scheutz 2005; Suhonen 1993). This type of plastic response to current predation risk has been seen in the form of reduced rates of parental nest visitation (Eggers *et al.* 2005; Ghalambor & Martin 2002; Martin & Ghalambor 1999; Muchai & du Plessis 2005; Strickland & Waite 2001) and increased parental incubation attentiveness (Fontaine & Martin 2006). Such a result is expected when high rates of nest visitation are likely to alert predators to the location of a nest (Skutch 1949). Thus, when nest predation risk is high, parents face a trade-off between placing their eggs or young in potential danger by visiting the nest frequently or by decreasing nest visitation rates and having their young starve or embryos die. One way to balance this trade-off with nestlings is to bring more food on each visit (Wright *et al.* 1998) and with eggs an increase in nest attentiveness could decrease the amount of activity that occurs around the nest (Conway & Martin 2000). Such changes in behavioural strategies should enable parents to visit the nest less frequently without compromising the health and safety of their young.

A number of studies have found that there can be high nest predation during the nestling stage (Liebezeit & George 2002; Yamaguchi & Higuchi 2005). This could be due to increased noise by the chicks (Briskie *et al.* 1994; Redondo & Castro 1992) and high rates of visitation to the nest by the parents (Martin *et al.* 2000a; Martin *et al.* 2000b; Muchai & du Plessis 2005; Schaefer *et al.* 2005). As nest predators can possibly locate nests by watching parents visit their nests (Liebezeit & George 2002), it is hypothesised that parents should decrease their visitation to the nest when nest predation risk is high (Skutch 1949).

Most studies of parental visit rates and nest attentiveness have been conducted on species that co-evolved with mammalian predators or in areas of high nest predation (Eggers *et al.* 2005; Ghalambor & Martin 2002; Martin & Ghalambor 1999; Muchai &

du Plessis 2005; Strickland & Waite 2001). However, it is not known how species that did not evolve with a high nest predation risk respond to varying levels of predation. The New Zealand avifauna offers an excellent model system for examining this issue. Native New Zealand birds did not evolve with predatory mammals and apart from a few native bird predators, they evolved in an environment that until recently had a relatively low risk of nest predation (Gill & Martinson 1991). Mammals were first introduced by Polynesians 1200 years ago and additional species were introduced by Europeans starting 200 years ago (Fleming 1962; Holdaway 1999; King 1984; King 1990). Europeans also brought an array of exotic bird species (Gill & Martinson 1991; Stevens *et al.* 1988). In contrast to the native birds, these introduced birds had a long evolutionary history with mammalian predators; as a result European bird populations have since thrived while native New Zealand bird populations have declined through high rates of mammalian predation (Duncan & Blackburn 2004; Moorhouse *et al.* 2003; Moors 1983; O'Donnell 1996; Wilson *et al.* 1998).

The objective of this chapter is to present an experiment in which I exposed both the native grey fantail (*Rhipidura fuliginosa*) and introduced song thrush (*Turdus philomelos*) to a model cat predator. My aim was to observe whether nest visitation rates and incubation attentiveness changed in response to the exposure of this model predator at the nest of each species. It is hypothesised that introduced birds like the song thrush should show a more dynamic response to the experimental predator's presence than native birds like the fantail, due to the former perceiving the predator as a threat from their evolutionary history with mammalian predators. In contrast, I expected the native fantail to show little changes in their behaviour as a result of evolving in an environment with no native mammalian predators.

Although it has been found that birds are generally less sensitive to mammalian predators when they have not coevolved with them (Lima & Dill 1990), it is not known if the reverse is true: that is, do birds gradually become less sensitive to predators when they are removed from their environment? In New Zealand a series of "mainland island" projects are being conducted to control mammalian predator populations. These are areas in which all (or most) introduced predators are controlled and thus provide an opportunity to test whether the response of both native and introduced birds changes with a decrease

in the risk of nest predation. In this study I used a "mainland island" near Kaikoura, New Zealand to determine whether birds become less sensitive to mammalian predators when they are removed and if there is a difference in response between introduced and native birds.

Methods

Study site

See Chapter 2 for a description of the two study sites. This included both Kowhai Bush, an area with little predator control, and Waiman Bush, an area with extensive control of rats (*Rattus norvegicus, R. exulans,* and *R. rattus*), cats (*Felis catus*) and mustelids (*Mustela furo, M. erminea,* and *M. nivalis*).

Study species

The species used in this experiment were grey fantails and song thrushes. Fantails are native to New Zealand while song thrushes were introduced in the late 1800's from Europe (Soper 1976). Both species have abundant populations within each study site.

Model predator

I used a taxidermic mount of a feral cat as a model predator. Cats are one of the mammals that were introduced to New Zealand that have become a significant threat to New Zealand birds (Fitzgerald & Veitch 1985). A cat was therefore an appropriate model for this experiment. Use of a taxidermic model allowed me to position the model in a similar manner near each nest. The model was posed in a life-like position and placed level with the nest so that it was looking directly at the nest. This simulated to the birds, via visual cues, that a predator had located their nesting site. I used two different taxidermic cat models to control for variations in model type and to check for problems with pseudoreplication. One cat was "orange" coloured while the other was slightly larger and was a grizzled grey and brown colour.

Video monitoring

Parental responses to the experimental nest predator were observed by the use of video recordings with Sony Hi8 video cameras. I tested nests both during the egg stage and during the nestling stage. Tests during the incubation period were only done on nests at least 5 days after the last egg was laid, in order to ensure that normal incubation behaviour was observed. Tests on nests with chicks were done only when their primary feathers began to break through their sheath. This controlled for developmental stage of the young since fantails and song thrushes have nestling periods that differ in length.

The filming of nests began in the morning within 1 hour of sunrise. Nests were first filmed for a 2 hour "control" period before the model was presented. At the end of the initial 2 hours, the cat model was then placed 2-4 meters away from the nest. The cat model was left in place for 15 minutes during which the video cameras were left running (I retreated out of the area to avoid confounding the response of the birds to the model with their response to my presence, although in most cases I could still hear if alarm calls were being given). From the recordings it was apparent that 15 minutes was generally enough time for parents to locate the predator. I then returned to the nest and removed the cat model and filming continued for another 2 hours to monitor parental responses "after" the model was presented. The camera was placed at least 10 m away from the nest and in all tests reported here, the parents did not appear to be affected by the presence of the camera. All tests and filming at a single nest was conducted on the same day to control for weather changes. Videos were later transcribed in the lab and visits to the nest before and after exposure to the cat model were recorded. For birds incubating eggs, I also recorded the percent of time spent incubating (termed attentiveness) before and after the model was presented. For each test, I also noted whether at least one adult alarm called during the model presentation, and if a bird returned to its nest during the time the model was in place. Control nests were also used in each study area to determine if time of day affected visitation rate or incubation attentiveness. Control nests were filmed over the same time of day as experimental nests but were not subject to model presentations.

Data analysis

The difference in nestling visitation, incubation attentiveness, and incubation visitation frequency before and after experimental model presentation was compared in both fantail and song thrush nests. Sample sizes varied between species and study areas due to availability of nests. Model presentation experiments during the incubation period were done on 2 song thrush nests and 7 fantail nests in Kowhai Bush, and 6 song thrush and 4 fantail nests in Waiman Bush. During the nestling period, model presentations were carried out at 9 song thrush nests in Kowhai Bush and 9 song thrush nests and 7 fantail nests in Waiman Bush. No fantails were available for filming in Kowhai Bush during the nestling period. In Waiman Bush, I used 5 song thrush and 5 fantail nests as controls during the nestling period, and 5 song thrush nests as controls during the nestling period in Kowhai Bush. During the incubation period, I used 5 song thrush and 6 fantail nests in Waiman Bush, and 5 song thrush and 5 fantail nests in Kowhai Bush.

Visitation rates and attentiveness (measured as percent time on the nest) before the model presentation were compared with the visitation and attentiveness rates after exposure. As the same nests were compared for before and after exposure periods, I initially used paired t-tests to compare each species in each study site for all the behaviours. I then combined all the data in a multifactor ANOVA for both species and both sites to test if there were differences in behaviours before and after exposure between the two sites. Site, species, and type of cat model (orange or grey) were used as factors. The response was the difference between visitation rates before and visitation rates after exposure to the model predator. As the type of cat used was not significant for any of the behaviours, I combined all data from each type of cat in all other comparisons. All data were normally distributed. The visitation rate to nestlings at Waiman Bush was not included in the ANOVA because no comparable data was available for fantails in Kowhai Bush.

Fisher exact tests were used to compare differences in alarm call rates between the two sites during the model presentation. This test was also conducted on whether or not normal visitation occurred during the exposure period. Normal visitation was defined as the adults returning to the nest to feed their chicks even when the model predator was

in place. There was not enough data to conduct this analysis on song thrushes during the incubation period.

Results

Initial reaction to cat model

I recorded the initial reaction of song thrushes to the cat model during the nestling period. In Kowhai Bush, only 1 out of 9 song thrushes (11%) visited its nest during the 15 minutes the model cat was presented while 6 out of 10 song thrushes (60%) in Waiman Bush visited their nest to feed chicks during the presentation of the model. This difference was significant (Fisher exact test: $p = 0.043$) and suggests that many thrushes in the area in which predators were controlled did not appear to recognize the cat as a threat. This result was confirmed when I compared whether or not song thrushes alarm called during the period in which the cat model was presented. In the study site at Kowhai Bush in which little predator control is undertaken, 8 out of 9 song thrushes (89%) alarm called during the model presentation while only 4 out of 10 song thrushes (40%) in Waiman Bush alarm called (Fisher exact test: $p = 0.038$).

Visitation rate and alarm calls during the model cat presentation were also examined for fantails in each study site. There was no significant difference in fantail visitation rate or alarm calls between the two sites (Fisher exact test: $p = 0.51$) during presentation of the cat model. In Kowhai Bush 6 out of 7 (86%) fantails showed normal visitation during the model exposure period, and 1 out of 7 (14%) fantails alarm called during model exposure. Furthermore, in Waiman Bush 3 out of 4 (75%) fantails visited the nest normally, and 1 out of 4 (25%) fantails alarm called during the model cat exposure.

Incubation visitation

There was no change in the rates of visits to the nest during the incubation period after the model presentation for either song thrushes ($t = -0.18$, $p = 0.86$) or fantails ($t = 2.29$, $p = 0.11$) in Waiman Bush or song thrushes ($t = -0.34$, $p = 0.79$) and fantails ($t = 1.12$, $p = 0.31$) in Kowhai Bush (Table 4.1). There was also no difference between the

two study sites in the degree of change between visits before and after the model cat presentation when compared using a multifactor ANOVA ($F_{1,14} = 0.008$, $p = 0.93$). Furthermore, control nests for song thrushes ($t = -0.45$, $p = 0.67$) and fantails ($t = -1.39$, $p = 0.22$) in Waiman Bush and song thrushes ($t = -2.77$, $p = 0.518$) and fantails ($t = 0.68$, $p = 0.54$) in Kowhai Bush did not show any significant change in visitation rate between early morning and mid-morning observation periods. The multifactor ANOVA for the control nests also did not show a significant difference between the sites ($F_{1,17} = 1.21$, $p = 0.29$), suggesting that the lack of a response was not masked by temporal changes in incubation visitation rates over the time frame of the experiment.

Incubation attentiveness

There was no change in incubation attentiveness after the model cat presentation for either species in either site. There was no difference in incubation attentiveness after model exposure for song thrushes ($t = -1.04$, $p = 0.34$) and fantails ($t = 0.55$, $p = 0.62$) in Waiman Bush or song thrushes ($t = 1.05$, $p = 0.49$) and fantails ($t = 0.92$, $p = 0.39$) in Kowhai Bush (Table 4.1). A multifactor ANOVA also showed no difference in incubation attentiveness before the presentation to incubation attentiveness after the presentation ($F_{1,14} = 1.1135$, $p = 0.31$). The control nests of song thrushes ($t = 0.62$, $p = 0.57$) and fantails ($t = -0.81$, $p = 0.45$) in Waiman Bush and control nests of song thrushes ($t = 0.02$, $p = 0.99$) and fantails ($t = 0.60$, $p = 0.58$) in Kowhai Bush also did not vary in levels of attentiveness in the early morning as compared to incubation attentiveness at mid-morning. This was also observed in the multifactor ANOVA ($F_{1,17} = 0.54$, $p = 0.47$).

Nestling visitation

It was expected that after exposure to the model cat, the rate of visitation to the nest would decrease. However, there was no significant change in the rate of visits to the nest after the model presentation in Kowhai Bush song thrushes ($t = -1.33$, $p = 0.221$), but there was a significant increase in the rate song thrushes visited their nests at Waiman Bush ($t = -4.42$, $p = 0.002$; Table 4.1; Figure 4.1). There was also a significant increase in visitation rate in fantails at Waiman Bush ($t = -4.44$, $p = 0.004$; Table 4.1; Figure 4.2). However, a multifactor ANOVA which compared the difference in visitation before and

after exposure between the two sites did not show that this difference was significant in the overall model ($F_{1,17} = 1.29$, $p = 0.274$).

Control nests of song thrushes and fantails in both sites were used to see if time of day had an effect on visitation rate. There was no difference in visitation rate observed for control song thrushes ($t = -1.28$, $p = 0.27$) and fantails ($t = -1.15$, $p = 0.31$) in Waiman Bush or song thrushes ($t = 0.38$, $p = 0.723$) in Kowhai Bush. There was also no difference in control nestling visitation before and after exposure when a multifactor ANOVA was conducted ($F_{1,8} = 1.44$, $p = 0.26$). The increase in visit rates observed after the model presentation in both song thrushes and fantails at Waiman Bush was not therefore due to increases in visitation rate that occur throughout the day.

Since birds may have responded to the model presentation on a much shorter time scale than the 2 hour interval I sampled, I re-examined my data by breaking down each observation period into 30 minute and 10 minute intervals to see if there was a discernable pattern in visitation rate. For example, birds may have reduced their visitation rate in the first half hour after the cat model was removed (as expected) but then increased it after this period to compensate, with the net result that no difference was apparent when the data were averaged over the entire observation period. However, no overall pattern was visible and none of the statistical results presented above change if only the 10 minutes before and after the model presentation were compared for song thrushes ($t = 1.44$, $p = 0.20$) and fantails ($t = -0.24$, $p = 0.83$) or if the same comparisons were done using a 30 minute interval for song thrushes ($t = -1.46$, $p = 0.20$) and fantails ($t = 0.59$, $p = 0.60$). Some individuals decreased visitation rates directly after model exposure and then dramatically increased later in the day, while other birds increased their visitation rate directly after the model presentation. Overall, there was no consistent trend observed.

Discussion

My results have shown that song thrushes and fantails in Waiman Bush and Kowhai Bush reacted differently to the model predator. Furthermore, this difference was observed during the period of model presentation. Birds in the predator control area where less likely to alarm call and more likely to visit the nest “normally” during the

model predator exposure period. This result suggests that birds in areas where predators are removed seem to be less likely to recognise predators which are being controlled as a threat.

Other studies have found that parents will increase their nest attentiveness (Fontaine & Martin 2006) and decrease nest visitation (Conway & Martin 2000; Eggers *et al.* 2005) when nest predation risk is high. However, in this study song thrush and fantail incubation attentiveness and incubation visitation before and after exposure did not differ significantly in either site. Some research has found that parental activity around the nest may not always increase nest predation rate (Farnsworth & Simons 1999; Schaefer *et al.* 2005). This could be the case in Waiman Bush. Species in a low nest predation risk environment may not change their behaviour immediately if a predator is spotted on very few occasions. There may be no need to change behaviour when predator encounter rate is low. However, as there was also no difference in incubation behaviour observed in Kowhai Bush species, this is an unlikely explanation.

In general, parents visit their nests less frequently during the incubation as compared to the nestling period, simply because of the increased demand of nestlings over that of eggs (Muchai & du Plessis 2005; Schaefer *et al.* 2005). Thus, it is possible that some the birds used in this study did not encounter the experimental predator during the 15 minutes I presented the model during nests tested at the incubation stage. Although in most model presentations it was likely at least one adult saw the model (i.e., alarm calls heard, or bird appeared on video tape), I cannot be sure that both parents were present. For example, if only a male song thrush saw the predator, the female may not have been aware of its presence and so would not be expected to alter its behaviour. It would therefore be beneficial to increase the exposure time to the model predator during the incubation stage to insure it is seen. As thrushes in particular will not return to the nest area when a human is nearby, it was not possible to confirm in most cases that the model was seen by the female. However, all the fantails used in this study did see the predator during model presentation and most individuals seemed to carry out normal visitation and attentiveness during the period when the model was present. Yet, two of the pairs (one in Kowhai Bush and one in Waiman Bush) altered their behaviour when the predator was near the nest. The pair in Waiman Bush was observed flying around the

nest alarm calling and would not sit on their eggs while the model was near. It was expected that fantails would not see the experimental predator as a threat due to their evolution without mammalian predators, however the altered behaviour of the two pairs suggests the fantails did feel threatened by the model. This result was not significant however; larger sample sizes would be beneficial to determine if fantails are showing an increased reaction to a model predator. It may be possible that some fantails have learned that mammals are a threat to their existence. Griffin *et al.* (2000) discovered anti-predator responses improve with experience. The fantails in New Zealand have been in contact with mammals for the past 1200 years, it therefore may be likely that some have learned that introduced mammals are predators, which could be the reason that fantail populations are still widely distributed around New Zealand.

There were low sample sizes in the incubation stage data for fantails and song thrushes. Larger sample sizes need to be obtained to see if there is a difference in nest attentiveness and incubation visitation when a predator is spotted near the nest. It is possible though that there is no immediate change in behaviour once the threat is gone and normal behaviour resumes when the predator is not seen. Changes may not occur in a matter of minutes, but as shown in chapter 3, continued exposure to predators (i.e. increased predation risk) over a few years time can cause changes in life history strategies to occur.

Significant changes in behaviour before and after exposure were observed in song thrushes and fantails in Waiman Bush during nestling visitation. However, these changes did not occur as was predicted. Song thrushes and fantails in Waiman Bush significantly increased their visitation to nestlings after the experimental predator was removed, whereas song thrushes in Kowhai Bush did not have any difference in behaviour after exposure. Yet, the song thrushes in Kowhai Bush alarmed called significantly more and more did not have "normal" visitation during the exposure period as compared to their Waiman Bush counterparts. It is possible that birds in Kowhai Bush would not have any difference in behaviour before and after the exposure period because these birds are constantly in high nest predation risk situations. It may not be uncommon to encounter a predator near their nest, therefore they would already be exhibiting the necessary anti-predator behaviours and visitation would not be expected to change. The song thrushes in

Kowhai Bush did alarm call significantly more than Waiman Bush song thrushes, therefore the Kowhai Bush song thrushes would not be expected to alter their behaviour after the experimental predator because they would presumably encounter predators on a daily basis, whereas Waiman Bush song thrushes would alter their behaviour after exposure because mammalian predators are not common. However, this does not explain why Waiman Bush song thrushes and fantails increased visitation rate after the model exposure. It was expected that if a change did occur it would be to decrease nest visitation after the predator presentation. An alternative explanation for the increased nestling visitation observed in Waiman Bush species is that they may be curious as to what is by their nest and may visit the nest more frequently to observe this unknown animal. Waiman Bush species may have lost the ability to recognise a cat as a threat due to predator control operations. The song thrushes and fantails in Waiman Bush may be visiting their nests more frequently after model presentation to examine the novel animal that is near their nest.

From the difference in alarm calls to the experimental predator, it is shown that Kowhai Bush song thrushes have an immediate response to a potential predator. Alarm calling did not occur as frequently in Waiman Bush song thrushes. Since predation risk is low in Waiman Bush, song thrushes may not alarm call when a predator is near their nest. It is likely that Waiman Bush species simply do not recognise the cat model as a threat; however why are the species visiting their nests more after the model is presented? From my data it is not known why song thrushes and fantails in Waiman Bush increased their visitation to the nest when predation risk was seemingly increased. It would be beneficial to collect data on the life expectancies of the bird populations within these two sites to observe if there could be changes in adult priorities when predators are removed from their environment (Curio 1988; Niethammer 1970).

This research has shown that the trade off involved in removing predators from a population is that there are reductions in response to a potential nest predator as displayed in Waiman Bush species based on alarm calling and rate of “normal” behaviour at the nest during the model presentation. Other behaviours that were expected to change did not change after the model exposure period. This may simply mean that birds resume their normal behaviour once a threat is removed. However, the behaviours that did

change changed in the opposite direction. It is possible that adults modify their priorities when control measures are taken in an area. When predators are removed adults may invest less energy in their current nesting attempt because there are higher chances of future broods; further research is needed to support this hypothesis. However the results have shown that it is important for predator control operations to continue in New Zealand due to the birds in these areas becoming accustomed to lowered predation risk and would have altered their behaviour in ways that would be detrimental if predators were reintroduced.

Table 4.1. Nestling visitation (visits/hour), incubation visitation (visits/hour), and incubation attentiveness (%) for song thrushes and fantails in Waiman Bush and Kowhai Bush before and after model predator presentation.

Species and Site	Before	After
Waiman Bush Song thrush		
Nestling visitation	7.49	10.07
Incubation visitation	1.78	1.84
Incubation attentiveness	48.28	61.40
Waiman Bush Fantail		
Nestling visitation	30.81	34.22
Incubation visitation	3.61	3.16
Incubation attentiveness	99.09	98.81
Kowhai Bush Song Thrush		
Nestling visitation	5.87	7.18
Incubation visitation	1.47	1.97
Incubation attentiveness	70.61	60.99
Kowhai Bush Fantail		
Incubation visitation	3.27	2.81
Incubation attentiveness	98.14	95.91

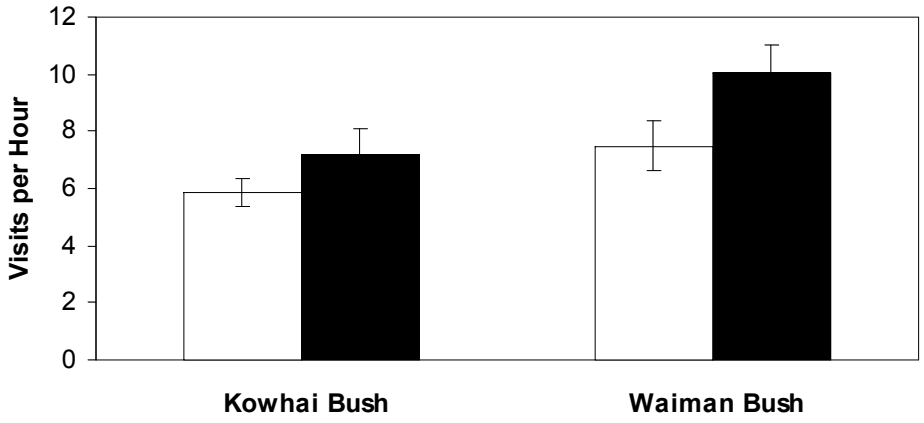

Figure 4.1. Visitation rates to feed nestlings of song thrushes before (white bars) and after (black bars) the experimental presentation of a model cat in Kowhai Bush (little predator control) and Waiman Bush (extensive predator control). Standard errors are shown.

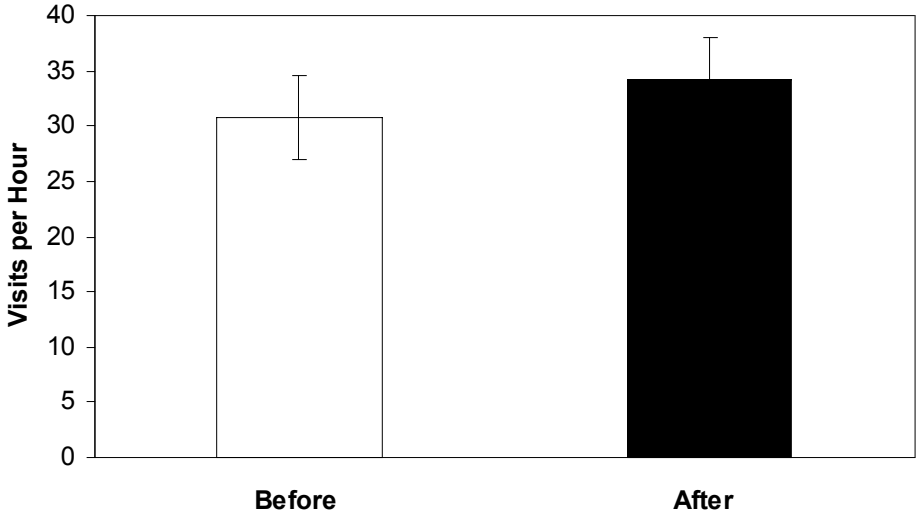

Figure 4.2. Visitation rates of fantails in Waiman Bush to feed nestlings before and after model cat exposure. Standard errors are shown.

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Chapter 5

General Discussion

Predation risk plays an important role in the shaping of life history strategies of birds (Doligez & Clobert 2003; Lima 1987; Ricklefs 1969). Birds are expected to behave in ways that reduce their overall risk of predation (Ferretti *et al.* 2005; Halupka 1998a; Halupka 1998b; Julliard *et al.* 1997; Koivula *et al.* 2002; Remeš & Martin 2002). Research has shown that birds display plasticity in their life history strategies, meaning that they are capable of short term changes in their behaviour (Conway & Martin 2000; Spaans *et al.* 1998). Plasticity enables changes in behaviours that lower predation risk (Lima & Dill 1990). New Zealand offers a unique environment for studying avian life history strategies. The native species did not evolve with mammalian predators while the introduced species present did (King 1984; King 1990). It is therefore expected that introduced species would be more flexible in their life history strategies since they came from an environment of very high predation risk. However, not all native species disappeared upon the introduction of exotic mammals, which implies that some native species may possess some plasticity in their life history strategies. The purpose of this thesis was to show how intensive mammalian control operations influence nest survival and the life history traits and behaviour of birds at their nests.

Mammalian predator control is an important tool in the conservation of New Zealand avifauna populations (Atkinson 2001). Many studies of mammal control in New Zealand focus on how endangered species are helped by this type of management (Innes *et al.* 1999; Moorhouse 1991; Moorhouse *et al.* 2003; Wilson *et al.* 1998). In contrast, there is little research on how more common New Zealand species are influenced by mammalian predator control (Kelly *et al.* 2005). In Chapter 2 I compared nest survival rates for common passerines between a site that has little predator control and a site that has intensive predator control. It was expected that mammalian predator control would cause an increase in avian survival rates. The results confirmed that both introduced and native birds in New Zealand had higher survival rates when mammalian predator control was present. However, the nest survival rates of the native species increased more than

the nest survival rates of introduced species. In the site with little mammal control, introduced species had a higher survival rate than native species. Conversely, in the mainland island site, native species had higher nest survival rates than the introduced species. These results show how mammalian predator control can significantly increase survival of native species that are relatively common.

Chapter 2 demonstrated that the two study sites used for this research had different levels of nest predation risk due to the differences displayed in overall nest survival rates. Birds are capable of changing their behaviours if predation risk is variable (Eggers *et al.* 2005; Martin *et al.* 2000). Therefore, these two sites provided an ideal opportunity to observe if there is plasticity in the life history strategies in New Zealand passerine populations. In this study, I focussed on six different life history traits, which included clutch size, length of the incubation period, length of the nestling period, rates of parental visitation to the eggs, incubation attentiveness, and rates of parental visitation to the nestlings. There was no difference observed in clutch size or incubation period between the sites. However, there were significant changes in nestling period, incubation attentiveness, visitation rates to the eggs, and visitation rates to the nestlings, at least in some species. From my analyses I found that there was no difference in the degree of change between introduced and native species; introduced and native species both changed their life history strategies in the same manner between the two sites.

The results from chapter 3 show that native New Zealand passerines may possess a degree of behavioural plasticity due to their being no difference in the degree of change observed in introduced species as compared to native species. The hypothesis that introduced species would be more plastic in their life history strategies than native species was thus not supported by these results. This could either be the result of inherent plasticity residing in native species throughout their evolutionary history (e.g. in response to native predators or other environmental factors) or it could be due to native species developing more plastic behaviours during the initial introduction of mammals and humans to New Zealand over 1000 years ago. Recently, Nussey et al. (2005) found that plasticity *per se* is a heritable trait and that selection has acted on the degree of plasticity in dates of first breeding in a great tit (*Parus major*) population in the Netherlands. This suggests that a greater degree of plasticity may have evolved in native species since the

introduction of exotic predators. Whether the degree of plasticity has changed in native birds in such a fashion is beyond the scope of this thesis, but the occurrence of several island populations of native birds that have never been exposed to exotic predators (e.g. bellbirds on the Poor Knights Islands) does provide a system for examining this question.

Another important result from chapter 3 was the short time frame in which changes in life history strategies apparently occurred. Predator control in the mainland island at Waiman Bush was only initiated in the past three years. This is likely to be within the life times of many of the birds present on the study area and too short for any large genetic changes to have occurred through selection. Instead, my study has shown that at least some life history traits in birds are capable of significantly changing in this short amount of time. This gives further evidence that birds are capable of monitoring their risk of nest predation and will change their behaviours when there is a change in nest predation risk.

From my results on changes in life history traits, the question arose as to whether or not birds will become less sensitive to mammalian predation if mammals are removed from their environment. In other words, does the response of a bird to a potential predator change in an environment where the chances of encountering a predator have become very small? The purpose of chapter 4 was thus to compare differences in behaviour to a potential nest predator between the two study sites. Three behavioural traits were used in this comparison, which included incubation attentiveness, adult incubation visitation rates, and adult nestling visitation rates. There was no difference in response to the predator observed in the incubation behaviours; however, there was a difference in nestling visitation. This difference was observed in the mainland island population of song thrushes and fantails. These two species increased their visitation directly after exposure to a potential nest predator. This was not the expected outcome; it was expected that if there was a change, the change would be a reduction in visitation rate after exposure to a nest predator.

Although I did not observe any significant changes in rates of visiting the nest or incubation the eggs in my model presentation experiments, I did find a strong difference between the two study sites in the response of the birds to the model itself. Song thrushes in the mainland island site were significantly less likely to alarm call to the predator and

significantly more likely to resume normal visitation to the nest during the exposure period. All birds except one, alarm called during the predator exposure in the high nest predation site. The same is true in normal visitation during the exposure period; only one parental pair visited the nest normally when the predator was present. These results have several possible interpretations. It is possible that the birds in the mainland island did not see the predator as a threat due to their removal from their environment. However, then there should not have been any difference in nestling visitation after exposure in this site since the control nests showed no change in visitation with regards to the time of day. The second possible interpretation is that the removal of mammalian predators has resulted in adult birds losing the ability to recognise mammals as a threat. Under this interpretation, intensive predator control has caused a decrease in the sensitivity of birds to mammalian predators. However, why there was then an increase in visitation after the model presentation is unclear. It is a problem that needs further work.

Birds in the mainland island site had a higher nest survival rate as shown from chapter 2; therefore it is possible that these birds also have a longer life expectancy. A longer life expectancy would imply that there are more chances of future breeding attempts and the parents would then focus more on their survival than their offspring's (Curio 1988). In order to support this hypothesis future research is needed to determine the life expectancies of the bird populations within the two study sites. If life expectancies are significantly longer in the mainland island it would then support the hypothesis that birds may change their investment strategies when mammalian predators are removed from their environment.

In conclusion, my study has shown that mammalian predator control increases the nest survival rate of most common native passerines and that even native New Zealand birds appear capable of changing their life history strategies in response to changing risks of predation by introduced predators. It has also been shown that birds appear to become less sensitive to mammalian predators when such predator populations are controlled. These findings have several implications for conservation management. It is important that once mammalian predator has begun it must be continued. If mammalian predators are reintroduced to a mainland island there may be detrimental consequences as the birds in such mainland islands are likely to have adopted a variety of behaviours associated

with a low risk of nest predation but which then place them at an increased risk of predation if predation are then reintroduced. Although I have found that birds can change a variety of nesting behaviours within a period of three years; it is not know how quickly birds are capable of reversing such behavioural changes to cope with a renewed risk of high predation. If changes in life history strategies induced by predator control increase the risk of mortality above a sustainable level when predators are reintroduced or reinvade, mammal control operations at mainland island projects may actually decrease the ability of native birds to adapt to introduced predators during periods in which predator control is relaxed. The ability of native birds to alter their life history strategies adds a new dimension to conservation efforts if such efforts in themselves change the way a bird responds to its environment. Understanding how birds change and adapt to their environment, including human-induced changes such as exotic introductions, will be vital if efficient and economic methods of predator control are to be expanded to conserve native birds on a larger spatial scale than that done to date.

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